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Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario K0G 1R0; (613) 269-3211; e-mail: fcook@achilles.net
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Cover: Female Canada Goose, *Branta canadensis*, on its nest showing typical incubating low profile posture. The nesting habitat is the typical early spring low grass meadows of the Saint Lawrence River islands. Note the presence of last year's dead vegetation with the new vegetation of the year. Taken on Ile aux Fermiers, Varennes, Quebec, by Martin Picard, Wildlife Biologist and Nature Photographer, 934 de la Rochelle, Boucherville, Quebec J4B 5M5 Canada. *See*: Establishment of a breeding population of Canada Geese, *Branta canadensis*, in southern Quebec by Jean-François Giroux, Josee Lefebvre, Luc Bélanger, Jean Rodrigue, and Stephane Lapointe, pages 75–81.

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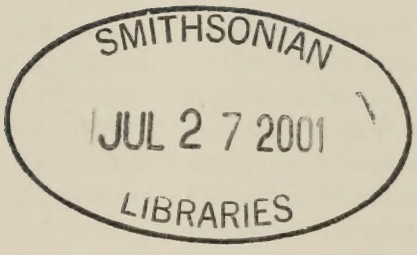

THE OTTAWA FIELD-NATURALISTS' CLUB

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Merriam's Shrew, *Sorex merriami*, and Preble's Shrew, *Sorex preblei*: Two New Mammals for Canada.

DAVID W. NAGORSEN[1], GEOFFREY G. E. SCUDDER[2], DAVID J. HUGGARD[3], HEATHER STEWART[1], and NICK PANTER[1]

[1]Royal British Columbia Museum, PO Box 9815, Station Provincial Govt, Victoria, British Columbia V8W 9W2, Canada
[2]Zoology Department, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[3]Centre for Applied Conservation Biology, Forest Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

Nagorsen, David W., Geoffrey G. E. Scudder, David J. Huggard, Heather Stewart, and Nick Panter. 2001. Merriam's Shrew, *Sorex merriami*, and Preble's Shrew, *Sorex prebli*: two new mammals for Canada. Canadian Field-Naturalist 115(1): 1–8.

A specimen of Merriam's Shrew (*Sorex merriami*) and three specimens of Preble's Shrew (*Sorex preblei*) were captured in pitfall traps set for terrestrial arthropods in the southern Okanagan Valley of British Columbia from 1995-1998. They represent the first captures of these mammals in Canada. The records are 130–300 km north of the nearest populations in Washington, but this distributional pattern probably reflects inadequate sampling. Both species were captured in shrub-steppe grassland habitats. Five species of shrews occur in the southern Okanagan Valley. To what extent they are syntopic in grassland habitats is unknown.

Key Words: Merriam's Shrew (*Sorex merriami*), Preble's Shrew (*Sorex preblei*), pitfall traps, sagebrush-steppe, distribution, Okanagan Valley, British Columbia, Washington.

The shrew fauna of Canada has been reviewed nationally (van Zyll de Jong 1983) and regionally (e.g., Nagorsen 1996). Nevertheless, most distributional data for these mammals are derived from general museum collecting or broadly focussed ecological inventories using conventional snap or live-traps. Williams and Braun (1983) and Corn and Bury (1987) demonstrated that pitfall traps are more effective for capturing insectivores and inventories based solely on snap or live-traps may fail to detect the small or rare shrew species in a community. Consquently, our understanding of the geographic distribution and habitat associations of shrews is rudimentary especially for the ecologically diverse Cordilleran region of western Canada.

Van Zyll de Jong (1983) speculated that Merriam's Shrew (*Sorex merriami*), Preble's Shrew (*Sorex preblei*), and the Dwarf Shrew (*Sorex nanus*), three species found in the western United States near the international boundary, could occur in western Canada. Recently, one of us (G. Scudder) captured one *S. merriami* and three *S. preblei* specimens in arthropod traps set in the Okanagan region of British Columbia. They represent the first captures of these species in Canada and extend their distributions considerably north of the nearest populations in Washington. Herein we describe the specimens, their habitat, and the biogeographic implications of these new records.

Study Area and Methods

Our study area was in the southern Okanagan region of British Columbia near the international boundary with Washington State. The area is bounded by the Cascade Mountains to the west and the Columbia Mountains to the east. Two major watersheds, the Okanagan River and Similkameen River, form narrow, low elevation (300 m) valleys separated by intervening rolling hills and low mountains (Figure 1). Situated in the rain-shadow of the coastal mountain ranges, the climate is dry and continental with wet springs, hot dry summers and variable winters (Cannings et al. 1987). Vegetation in the low valleys consists of shrub-steppe grassland and narrow strips of riparian habitat bordering lakes and rivers. Hills and lower slopes of mountains support open parkland habitats with scattered Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). The region has been affected by cattle grazing, irrigation for agriculture, and urban development (Cannings et. al. 1987;* Bryan 1996*).

*See Documents Cited Section

The new shrew records were part of a sample of small mammals captured incidentally in pitfall traps for capturing terrestrial arthropods that were set in 20 study sites in the south Okanagan Valley from 1993–1998. Rings of five traps were placed at 50 m intervals along vegetational transects to sample specific biophysical habitats. Each trap ring was 10 m in diameter; the five traps were placed in a pentagonal pattern at the periphery of the ring. The traps consisted of two plastic beakers (beer mugs) with a top diameter of 8.5 cm and depth of 11 cm. One beaker was set in the ground with the top level to the soil surface; the other beaker, snug-fitting into the first, was one-third filled with 50% propylene glycol. We checked and emptied traps at monthly intervals from April to October but we left traps unchecked from October to April. As a result, the precise capture date could not be determined for shrews. A total of 24 shrews were captured in 20 different traps from 14 study sites.

We identified shrew specimens from dental and cranial traits using the keys and diagnostic traits given by Diersing and Hoffmeister (1977), Junge and Hoffmann (1981), Carraway (1995), and Nagorsen (1996). We measured condylobasal length with Helios dial calipers; other cranial measurements were taken with an ocular micrometer. For the four specimens suspected to be *S. merriami* or *S. preblei*, we extracted and cleaned their skulls. Their carcasses and skulls are stored as voucher specimens in the collections of the Royal British Columbia Museum (RBCM). We confirmed our identification of *S. merriami* from reference specimens borrowed from the Connor Museum, Washington State University. The three specimens identified as *S. preblei* were sent to Lesley Carraway at Oregon State University for verification.

For the *S. merriami* and *S. preblei* sites, we recorded the dominant plant species, slope, latitude, longitude, elevation, percent shrub cover, distance to nearest tree, and distance to standing water at each site. Percent shrub cover estimates were based on 10 m × 10 m plots using the methods described by the British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks (1998*). Slope was calculated using the percent scale of a SUUNTO® clinometre. Aspect was recorded as the orientation of the slope measured in degrees by compass. The nearest tree to each trap site was measured with a 100-m steel tape. We estimated distance to nearest standing water from topographic maps. We calculated coordinates and elevation (x, y, and z) with a CMT-GPS® Global Positioning System device. The biogeoclimatic zone ecosystem classification for sites was described by Meidinger and Pojar (1991*); ecosystems were based on habitat polygons mapped by the British Columbia Ministry of Environment, Lands and Parks. Plant names follow Douglas et al. (1994*).

Results

Sorex merriami

RBCM 19982 (Table 1), was positively identified as *S. merriami* by the absence of medial tines on the first pair of upper incisor teeth. Other diagnostic traits included the third upper unicuspid tooth larger than the fourth and the presence of a postmandibular foramen on the rami of the mandibles. Measurements are consistent with those described by Diersing and Hoffmeister (1977) for a sample of 53 individuals from Washington State (Table 2). The specimen was an adult female captured in summer (14 July–16 August 1996).

The trap site (KL1-1) was about 0.5 km NW of Kilpoola Lake south of Richter Pass (Figures 1, 2; Table 1) in sagebrush rangeland. The biogeoclimatic zone ecosystem classification for this site is: Ponderosa Pine zone, very dry hot subzone (PPxh1). Although now protected as a special management area with cattle excluded by fencing, the area was heavily grazed until the early 1990s. Shrub cover was sparse (5%) consisting equally of Big Sagebrush (*Artemisia tridentata*) and Threetip Sagebrush (*Artemisia tripartita*) less than 1 m high. Grasses were dominant (> 50%) at the site and included: Fowl Bluegrass (*Poa palustris*), Japanese Brome (*Bromus japonicus*), and Columbian Needlegrass (*Stipa nelsonii* var *doreii*). Forbs included: Timber Milkvetch (*Astragalus miser*), Parsnip-flowered Buckwheat (*Eriogonum heracleioides*), Yarrow (*Achillea millefolium*), and Meadow Death Camas (*Zigadenus venenosus*). There was no tree overstory; a stand of Trembling Aspen (*Populus tremuloides*) was situated about 75 m from the site. Nearest standing water was about 0.5 km away at Kilpoola Lake. No other shrews were captured at this site.

Sorex preblei

RBCM 19993, 20005, and 2006 were clearly members of the *Sorex cinereus* group with medial tines present on the edge of their first upper incisors and their third upper unicuspid teeth equal to or larger in size than the fourth unicuspids. We identified them as *S. preblei* from their short skulls, mandibles, and rostrums; and flat braincases. Measurements (Table 3) are consistent with those described by Cornely et al. (1992) and Carraway (1995). RBCM 19993 was an old adult of unknown sex captured 9 July–10 August 1995. RBCM 20005 and 2006 were captured between 5 October 1994–9 April 1995. RBCM 20005 was a subadult female; RBCM 2006 was a young adult male.

The three *Sorex preblei* were taken from three separate sites: K3-2, Y5-2, and Z3-1 (Table 1). Trap site K3-2 (Figures 1, 3; Table 1) was on the south slope of Mt. Kobau, north of Richter Pass. The biogeoclimatic zone ecosystem classification for this site is: Interior Douglas-fir zone, wetter subzone (IDFdk1). The area was moderately grazed by cattle. The trap station was

TABLE 1. Habitat and geographic data for capture sites of three Preble's Shrews (*Sorex preblei*) and a Merriam's Shrew (*Sorex merriami*) from the southern Okanagan Valley of British Columbia.

Species	RBCM#	Site	Location	Latitude	Longitude	Elevation	Slope	Aspect	Shrub Cover
S. merriami	19982	KL1-1	Kilpoola Lake	49°02'0.31''N	119°33'56.90"W	827 m	-8%	123°	5%
S. preblei	19993	K3-2	Mt. Kobau	49°06'12.37''N	119°40'22.69"W	1724 m	-35%	148°	80%
S. preblei	20006	Y5-2	Vaseux Creek	49°16'5.10"N	119°30'55.43"W	343 m	-26%	312°	40%
S. preblei	20005	23-1	Vaseux Creek	49°15'38.98''N	119°30'32.39'N	452 m	-55%	270°	30%

in a patch of open grassland surrounded by scattered stands of Douglas-fir. Big Sagebrush (*Artemisia tridentata*) and scattered Snowberry (*Symphiocarpus albus*) about 1 m in height formed a dense shrub cover (80%). Under this dense cover, grasses were dominant and included Bluebunch Wheatgrass (*Elymus spicata*), Idaho Fescue (*Festuca idahoensis*), Columbian Needlegrass (*Stipa nelsonii* var *doreii*) and Junegrass (*Koeleria micrantha*). Forbs included Nettle-leaved Giant Hyssop (*Agastache utriculfolia*), Parsnip-flowered Buckwheat (*Erigonum heracleoides*), Old Man's Whiskers (*Geum triflorum*) and Fern-leaved Desert-parsley (*Lomatium dissectum*), Yellow Penstemon (*Penstemon confertus*). There was no tree overstory but scattered Douglas-fir trees were 13 m from the trap site. Nearest known standing water was at least 2.3 km from the site. The Dusky Shrew (*Sorex monticolus*) and Vagrant Shrew (*Sorex vagrans*) were also taken at this trap station and several other trap sites on Mt. Kobau.

Trap site Y5-2 (Figure 1, Table 1) was on a bench about 0.9 km southeast of Vaseux Lake in the Vaseux-Bighorn National Wildlife Area. The biogeoclimatic zone ecosystem classification for this site is: Bunchgrass zone, very dry hot subzone (BGxh1). According to Krannitz (1997) the site was grazed by cattle and horses until 1996; the area is still grazed by various wildlife species including Bighorn Sheep (*Ovis canadensis*). Antelope Bush (*Purshia tridentata*) about 2 to 2.2 m high formed a dense shrub cover (40%). Cheatgrass (*Bromus tectorum*) is the most widespread herbaceous plant at the site (Krannitz, unpublished data) with Diffuse Knapweed (*Centaurea diffusa*) the second most common plant species. Other grasses include Needle-and-thread grass (*Stipa comata*) and Sand Dropseed (*Sporobolus cryptandrus*). Other forbs included Annual Jacob's Ladder (*Polemonium micranthum*), Small-flowered Blue-eyed Mary (*Collinsia parviflora*) and Brittle Prickly-Pear Cactus (*Opuntia fragilis*). There was no tree overstory but scattered Ponderosa Pine occurred 15 m from the trap site. Nearest standing water was at Vaseux Lake 0.9 km from the site. No other shrews were captured in this study site.

Trap site Z3-1 (Figures 1, 4; Table 1) was on a bench about 1.7 southeast of Vaseux Lake. Habitat and the biogeoclimatic zone classification at this site was similar to trap site Y5-2. Although grazed by wildlife species, historically the site has had little grazing from domestic livestock (Krannitz 1997). Antelope Bush about 1.5–1.7 m high formed a dense shrub cover (30%). Cheatgrass was the dominant plant cover with Blue Forget-me-not (*Myosotis stricta*) almost as common. Other grasses included Needle and thread grass, Six-weeks Fescue (*Vulpia octoflora*) and Sandberg's Bluegrass (*Poa secunda*). There was no tree overstory and the nearest trees were scattered Ponderosa Pine about 40 m from the site. Nearest standing water was at Vaseux Creek, about 350 m from the trap site. No other shrews were captured in this study site.

Discussion

Associated with the arid grasslands of western

TABLE 2. Measurements (mean, range) for Merriam's Shrews (*Sorex merriami*) from Washington State and the specimen from British Columbia.

Measurement	RBCM 19982	Washington[a]
Tail length	33	36 (30–43)
Hind foot length	14	12 (11–14)
Skull length	16.1	15.7 (15.1–16.1)
Braincase breadth	8.9	8.3 (7.8–8.3)
Unicuspid toothrow length	1.9	2.0 (1.8–2.2)
Breadth across 2nd unicuspids	2.0	2.1 (2.0–2.4)
Breadth across 3rd upper molars	4.3	4.4 (4.1–4.7)
Breadth across 4th upper premolars	4.4	4.3 (4.0-4.6)

[a]based on a sample of 53 specimens taken from Diersing and Hoffmeister (1977).

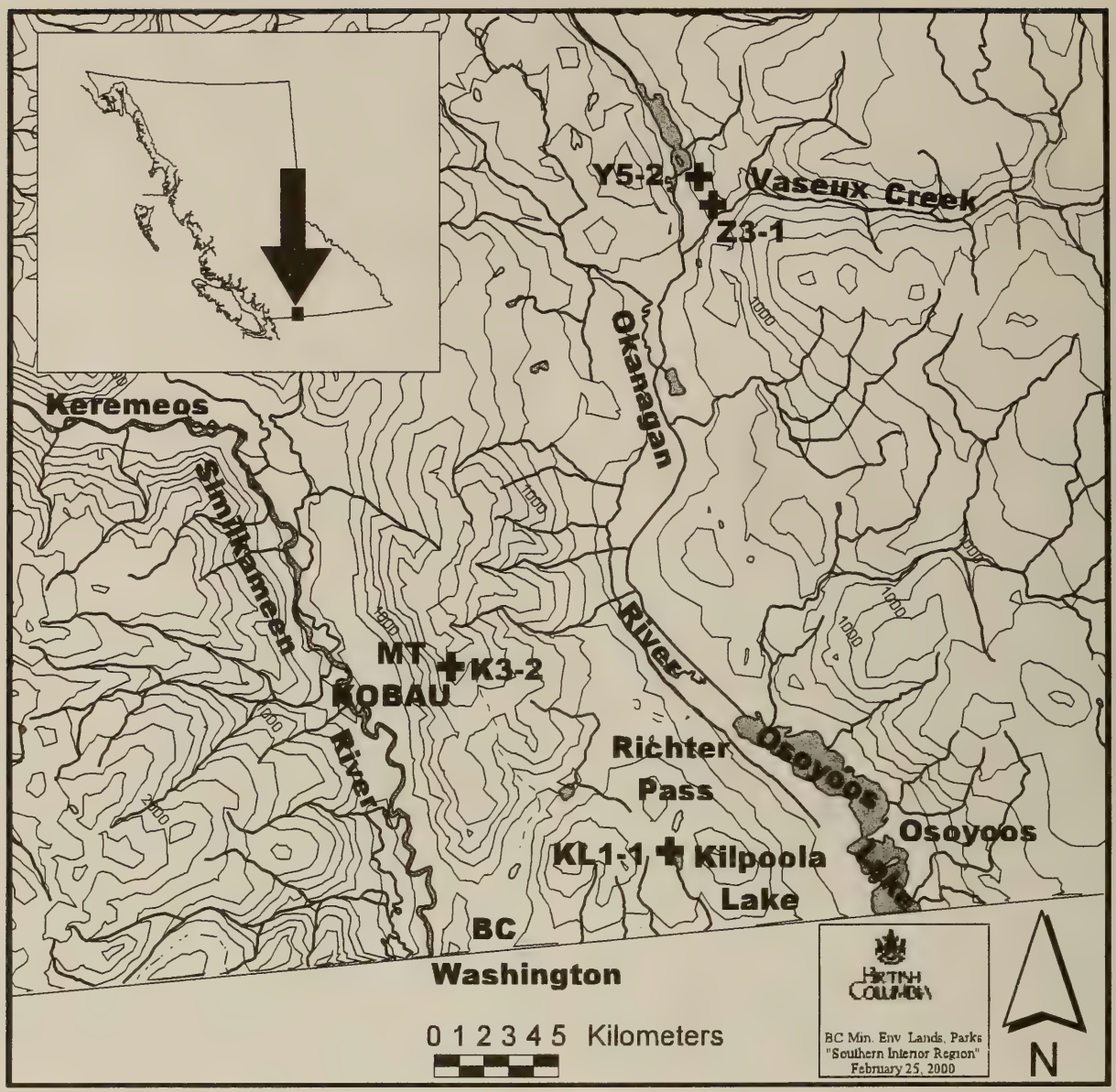

FIGURE 1. The southern Okanagan Valley region of British Columbia and locations of the shrew collecting sites.

North America, *S. merriami* is one of the most xeric-adapted of all North American shrews (Junge and Hoffmann 1981). In Washington where this species inhabits the Columbia Basin, it is mainly associated with Big Sage and Bunchgrass habitats (Johnson and Clanton 1954; Johnson and Cassidy 1997*). The British Columbian record is in similar habitat, and the Kilpoola Lake site is part of one of the largest tracts of sagebrush grassland remaining in the southern Okanagan Valley (Bryan 1996*). Although Johnson and Clanton (1954) and Johnson and Cassidy (1997*) reported that *S. merriami* is always found in runways and burrows of the Sagebrush Vole (*Lemmiscus curtatus*), this vole is absent from British Columbia. However, in British Columbia *S. merriami* may use runways of the Montane Vole (*Microtus montanus*), the most common arvicoline rodent in the intermontane grasslands of southern British Columbia. Nagorsen (1995*) reported *M. montanus* in grassland habitat near the *S. merriami* site.

Irregularly distributed throughout the Columbia Plateau, Great Basin, and Great Plains, *S. preblei* is associated with a wider variety of habitats than *S. merriami*. In the Blue Mountains of Washington, *S. preblei* was found at 1525–1830 m elevation in dense forests of Lodgepole Pine (*Pinus contorta*), Subalpine Fir (*Abies lasiocarpa*)-Lodgepole Pine, and Grand Fir (*Abies grandis*)-Englemann Spruce (*Picea engelmanii*) (Armstrong 1957). However, these habitats are atypical. In other regions of the western United States *S. preblei* inhabits arid steppe-grassland, montane forest, riparian areas, and seasonally wet sagebrush communities (Ports and George 1990; Cornely et al. 1992). Sagebrush and Antelope Bush are often mentioned in habitat descriptions for this species. The three *S. preblei* from British Columbia were taken in two distinct commu-

FIGURE 2. Merriam's Shrew (*Sorex merriami*) capture site (KL1-1) at Kilpoola Lake, British Columbia. Photo taken 11 July 1999 by D. W. Nagorsen.

nities: a low elevation Bunchgrass-Antelope Bush community and a montane Sagebrush- Interior Douglas-fir community. These communities shared the common habitat attributes of a dense shrub cover and no tree overstory.

The *S. merriami* and *S. preblei* records from British Columbia appear to be isolated from the nearest populations in Washington, but this distributional pattern may largely reflect inadequate sampling particularly in regions adjacent to the international border. Because both species are rare and usually captured in pitfall traps, they may escape detection in general mammal surveys. The nearest known population of *S. merriami* is 130 km south in the Columbia River basin. According to Johnson and Cassidy (1997*), the species is unknown from the west side of the Columbia River north of Ellensburg or Vantage in Washington. Nevertheless, only three shrew specimens have been taken from Okanagan County (Johnson, personal communication), the county adjacent to the Okanagan Valley of British Columbia. With suitable bunchgrass-sagebrush habitat found throughout the Okanagan River valley in Washington, it seems likely that the British Columbian population of *S. merriami* is linked to the Columbia Basin population via intervening populations. The

TABLE 3. Measurements (mean, range) for Preble's Shrew (*Sorex preblei*) from Oregon and three specimens from British Columbia.

Measurement	RBCM 19993	RBCM 20006	RBCM 20005	Oregon[a]
Total length	–	77	76	91 (75–99)
Tail length	–	33	32	36 (29–40)
Skull length	14.0	14.3	14.5	14.4 (13.2–14.8)
Maxillary breadth	4.1	4.2	4.3	4.0 (3.8–4.2)
Maxillary toothrow length	5.5	5.4	5.5	5.1 (4.7–5.4)
Dentary length	6.3	6.1	5.8	6.2 (5.7–6.8)
Length of mandibular toothrow	4.1	4.2	4.3	4.0 (3.8–4.1)

[a]based on a sample of 15 males from Verts and Carraway (1998)

FIGURE 3. Preble's Shrew (*Sorex preblei*) capture site (K3-2) at Mt. Kobau, British Columbia. Photo taken 9 September 1999 by D. W. Nagorsen.

distribution of *S. preblei* is more puzzling. The nearest population to British Columbia is more than 300 km south in the Blue Mountains of eastern Washington. Johnson and Cassidy (1997*) developed a model for this species' distribution based on GIS analysis, but they emphasized that the status of *S. preblei* in Washington was essentially unknown. Verts and Carraway (1998) suspected that the few records for this species probably result from sampling effort. Clearly comprehensive inventories employing pitfall traps are required to delimit this species' distribution in Washington and British Columbia. We also note that there are records of *S. merriami* and *S. preblei* from northern Montana (Diersing and Hoffmeister 1977; Cornely et al. 1992) and both species could occur in southern Alberta.

Although sagebrush-steppe habitats generally support low population densities of shrews, species richness may be high in these habitats. As many as five shrew species coexisted in some of the sagebrush-steppe communities studied by Kirkland et al. (1997). Shrew assemblages associated with the intermontane grasslands of British Columbia are poorly known. Four species were recovered in our pitfall traps: *S. merriami*, *S. monticolus*, *S. preblei*, and *S. vagrans* with *S. monticolus* and *S. vagrans* accounting for 83% of the 24 shrew captures. Curiously, we did not trap the Common Shrew (*Sorex cinereus*), yet Kirkland et al. (1997) found it to be the dominant shrew in sagebrush-steppe habitats in Wyoming. There are historical museum records of *S. cinereus* from Penticton, Summerland, and Okanagan Landing in the Okanagan Valley of British Columbia (Nagorsen 1996) but they lack habitat data. To what extent these five species are syntopic in southern British Columbia is not clear. We trapped only one shrew species at most of our study sites, but *S. preblei*, *S. monticolus*, and *S. vagrans* were taken in the same trap station at one of the Mt. Kobau study sites. Our results should be viewed with caution as we used only a few pitfall traps in each study site. Kirkland et al. (1997) employed arrays of three trap lines of 25 pitfall traps each for a total sampling of 514 060 trap days. A similar sampling effort will be required to delimit shrew communities associated with the grasslands of the southern Okanagan Valley.

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FIGURE 4. Preble's Shrew (*Sorex preblei*) capture site (Z3-1) at the Kennedy bench near Vaseux Lake, British Columbia. Photo taken 9 September 1999 by D. W. Nagorsen.

her vegetational data for the Vaseux Creek sites, F. Sachedina for preparing the map with GIS software, L. Carraway for confirming our identifications of the three *S. preblei*, and R. Johnson for providing a loan of *S. merriami* specimens and his unpublished data on Washington shrews. We are particularly grateful to O. Dyer for his support and assistance in various aspects of the study. Our research was supported by the Royal British Columbia Museum and by grants to G. G. E. Scudder from Forest Renewal British Columbia and the Natural Sciences and Engineering Research Council of Canada.

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Effects of Beaver, *Castor canadensis*, Herbivory on Streamside Vegetation in a Northern Ontario Watershed

D. M. Barnes[1] and A. U. Mallik[2]

[1]Department of Biology/Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada
[2]Department of Biology, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada

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Based on the life-form and their utility to Beavers (*Castor canadensis*), we classified the riparian plants around Beaver impoundments into five categories: Alder (*Alnus* spp.) — dam construction; Trembling Aspen (*Populus tremuloides*) — primary food; White Birch (*Betula papyrifera*) and Willows (*Salix* spp.) — secondary foods; shrubs — occasionally used for food and dam construction; and conifers — occasionally used for dam construction. To study the influence of Beaver herbivory on shoreline woody plants, we randomly chose eight recently active (< 5 years since establishment), seven recently abandoned (< 12 years since abandonment), and eight old abandoned (> 12 years since abandonment) dam sites. We found that Beavers concentrated the majority of their herbivory to within 20 m of the impoundment edge. Three explanations are proposed: (1) thermoregulatory restrictions; (2) directionally leaning trees within riparian habitats; and (3) reduction of predation risk. After 12+ years of abandonment, we found the Beaver's preferred food tree, the Trembling Aspen, had not re-established along streams adjacent to abandoned dam sites. In contrast, less desirable food trees and conifers showed increased recovery. If this selective herbivory continues unchecked, the riparian habitat along the Swanson River will become dominated by conifers and thus unsuitable for sustaining Beavers. We believe that fire is needed to rejuvenate the failing Trembling Aspen stocks.

Key Words: Beaver, boreal forest, *Castor canadensis*, foraging distance, woody vegetation, predation, Ontario.

Johnston and Naiman (1990) suggested that of all the North American herbivores, Beavers (*Castor canadensis*) have the greatest potential to affect plant communities. They provided three reasons why Beaver herbivory may have such a large impact: (1) Beavers cut down trees and shrubs, thus affecting the canopy and sub-canopy light levels of forests; (2) Beavers restrict their cutting activity to narrow, riparian habitats, thus concentrating the impact along the shorelines; and (3) Beavers harvest trees in excess of their nutritional needs.

As central-place foragers, Beavers focus their foraging activities around a central water-based colony (Basey and Jenkins 1995). In northern Ontario, Beavers rely heavily on riparian plants for food acquisition and dam construction and maintenance. Trembling Aspen (*Populus tremuloides*) is considered to be their primary food, with Willow (*Salix* spp.) and White Birch (*Betula papyrifera*) being of secondary importance. To a lesser degree Beavers will also make use of deciduous shrubs, such as Pin Cherry (*Prunus pensylvanica*), Mountain Maple (*Acer spicatum*), Red Osier Dogwood (*Cornus stolonifera*), Mountain Ash (*Sorbus americana*), Choke Cherry (*Prunus virginiana*), Serviceberry (*Amelanchier* spp.), Beaked Hazel (*Corylus cornuta*), and River Birch (*Betula glandulosa*). Beavers, also, use riparian plants for dam construction, most notably Alder (*Alnus* spp.) although deciduous shrubs and conifer species are occasionally used (Barnes and Mallik 1996).

Most Beaver research has concentrated on food foraging (Chabreck 1958; Hall 1960; Brenner 1962; Nixon and Ely 1969; Northcott 1971; Jenkins 1980; Belovsky 1984; McGinley and Whitham 1985; Fryxell 1992). Research dealing with the overall effects of Beaver herbivory on plant communities has largely been restricted to a few studies: western Wisconsin (Barnes and Dibble 1988); northern Minnesota (Johnston and Naiman 1990); and eastern Ontario (Donkor and Fryxell 1999, 2000). With the exception of Donkor and Fryxell (1999, 2000), who studied one 3-year-old abandoned dam, these studies largely based their analysis on data collected at active beaver colonies.

Despite the many studies that have been devoted to abandoned Beaver dams, no study has quantitatively assessed the recovery of woody plants adjacent to abandoned impoundments over an extended period of time. For the most part this research has focused on two main aspects of abandoned dams: (1) the plant regeneration within the abandoned basin of impoundments (Morgan 1868; Rudemann and Schoonmaker 1938; Ives 1942; Wilde et al. 1950; Knudsen 1954; Neff 1957; Naiman et al. 1988; Terwillger and Pastor 1999); and (2) the effects on wildlife (Beard 1953; Neff 1957; Rutherford 1964; Hodkinson 1975; Novak 1987; Terwillger and Pastor 1999).

To address these research needs, our present study focused on the Swanson River, an entire watershed area within the Chapleau Crown Game Preserve of northern Ontario. The specific objectives of the study were to: (1) determine the effect of Beaver herbivory on shoreline woody plants at recently active dam sites; (2) to assess the recovery of shoreline woody plants at abandoned Beaver dams; and (3) to determine if prolonged foraging by Beavers had any effect on species richness, diversity, and evenness of streamside woody plant communities.

Study Area

The study was conducted within the Swanson River drainage basin of the Chapleau Crown Game Preserve (48°05′N, 83°20′W; elevation range 348 – 510 m asl [above sea-level]; area of 700 000 ha) of northern Ontario (Figure 1). The Swanson River has a 200 km network of streams covering an area of 228 km^2 (Figure 1). Alder dominated riparian habitats. The forests were dominated by Jack Pine (*Pinus banksiana*) and Black Spruce (*Picea mariana*) interspersed with mixed stands of White Spruce (*Picea glauca*), Balsam Fir (*Abies balsamea*), White Birch and Trembling Aspen. Associated with these forest trees were numerous understory trees and shrubs such as Willow, Pin Cherry, Mountain Maple, Dogwood, Mountain Ash, Choke Cherry, Black Ash (*Fraxinus nigra*), Serviceberry, Beaked Hazel, and River Birch.

Since its inception in 1925, there has been a ban on all hunting and trapping in the preserve (Anonymous 1985). Although there have been notable exceptions of this policy (i.e. road-side removals of nuisance beavers and translocation of Beavers to rehabilitate depleted populations throughout Ontario), no Beavers were trapped during the spring and summer of 1992 and 1993 (C. Todesco, Ontario Ministry of Natural Resources, Chapleau ON, personal communication). As a further precaution, no active dam was selected for study if that dam bordered on a road.

Logging has been an ever-present activity within the Preserve. Between 1910 and 1940, timber-harvesting operations were concentrated around railway communities. By the early 1940s most of the easily accessible timber was harvested and transported by river or rail (Anonymous 1985). To access inland timber resources, road based operations were begun and have persisted to present day. Between 1948 and 1958, salvage operations were started on a number of large fires near Racine Lake (45 000 ha) (Anonymous 1985). Since the 1950s, the Swanson River watershed has received very little harvesting activity. From 1975 to 1995, all cutting was done on the north, east, and south peripheries of the Swanson River watershed (B. Riche, Ontario Ministry of Natural Resources at Chapleau, Ontario, personal communication; Figure 1). We observed no cutting activity around any of the active Beaver dams analyzed.

Based on trapping and logging history, we are confident that the Swanson River watershed provided a natural forest setting where Beavers were studied without major human disturbance.

Methods

The Swanson River system was sub-divided into 200 1-km sections (Barnes and Mallik 1997). A total of 40 stream sections were classed as active (at least one active dammed colony), 85 as abandoned (at least one abandoned dammed colony with no evidence of active dams), and 75 as no-dam sites (no dam building activity evident). Beaver impoundments were located by aerial survey (Cessna 180) in the autumn of 1991 (Bergerud and Miller 1977) and a stereoscopic examination of 1980 (R:F-1:15840) and 1992 (R:F-1:8000) aerial photographs. From these 200 sites, 15 active, 15 abandoned, and 12 no-dam sites were randomly chosen. Since some of the sample sites were remote, the selection process involved assessing the site's accessibility. To ensure that the data could be completed by September, we chose only those sites in which data could be collected in one day (Barnes and Mallik 1997).

An active Beaver dam that has been active for an extended period of time can differ significantly from a newly formed site. To address this concern, we used only recently established dams (< 5 years since creation). Eight active sites were classed as "recently active" based on the longevity of flooded Alder. Swank (1949) found that Alder survived only two to four years after being flooded. Using this technique, we chose only those active impoundments in which the flooded Alder were alive. Further, we sub-divided the abandoned dam sites into seven recently abandoned (< 12 years since abandonment), and eight old abandoned (> 12 years since abandonment) sites (Figure 1). Using aerial photography, time since abandonment was arbitrarily assessed as being recent or old. An impoundment was classed as recently abandoned if there was no evidence of the impoundment on the 1980 aerial photos and if the impoundment viewed in the 1992 aerial photos showed evidence of being abandoned; i.e., broken dams, presence of Beaver meadows (Wilde et al. 1950), presence of dead trees, and a reduced water level in the impoundment. Old abandoned dam sites were those, which appeared in the 1980 aerial photos as being abandoned.

To assess the effect of Beaver herbivory on shoreline woody plant communities, we collected utilization/availability data at the eight recently active impoundment sites. To select which of the two impoundment shorelines to analyze, we placed two pieces of paper representing each shoreline into a cap and randomly chose one. Along the chosen shoreline, a sample plot was established with a

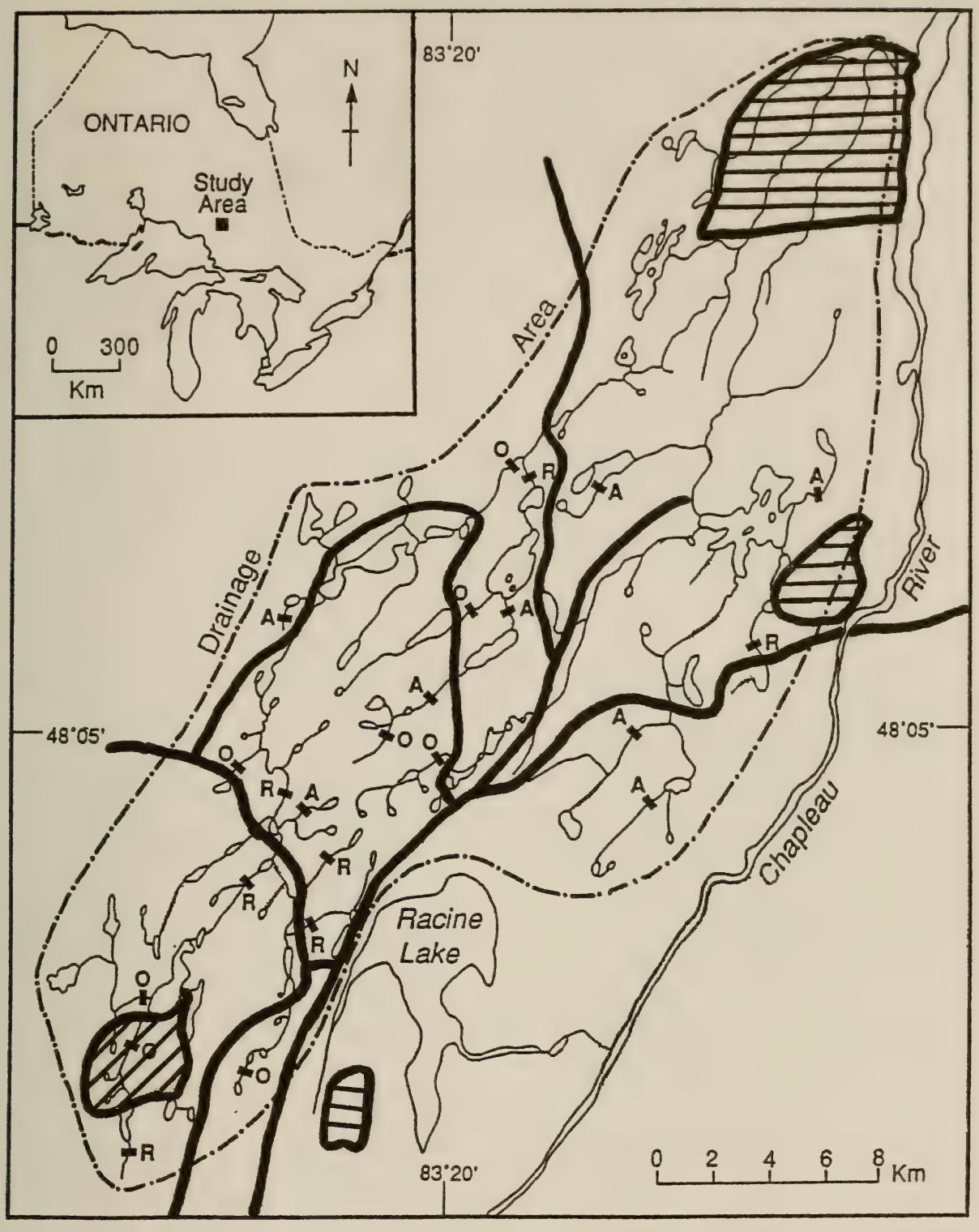

FIGURE 1. The Swanson River drainage basin study area with the location of recently active (A), recently abandoned (R), and old abandoned (O) Beaver impoundments sampled. Location of the Chapleau Crown Game Preserve study area in Ontario is shown in the inset. Also included is the network of gravel roads (solid dark lines) and areas logged between 1975 – 1985, ▤ and 1985 – 1995, ▨.

width and length of 40 m and 170 m, respectively (Barnes and Mallik 1997) (Figure 2). We randomly chose three shoreline locations within the sampling plot. At each of these locations, a 1 m × 40 m belt transect was established perpendicular to the impoundment's edge. Each transect was sub-divided into 40 - 1 m × 1 m sub-plots (Figure 2). We measured all Beaver-cut stumps and uncut stems with diameters ≥ 0.5 cm along the 24 – belt transects of the eight recently active impoundments. Diameter measurements of Beaver stumps were measured at the point cutting was initiated. For standing trees and shrubs, diameters were taken 30 cm above the ground (Johnston and Naiman 1990; Barnes and Mallik 1996). Because of the low number of cut stems encountered in each transect, the total stem

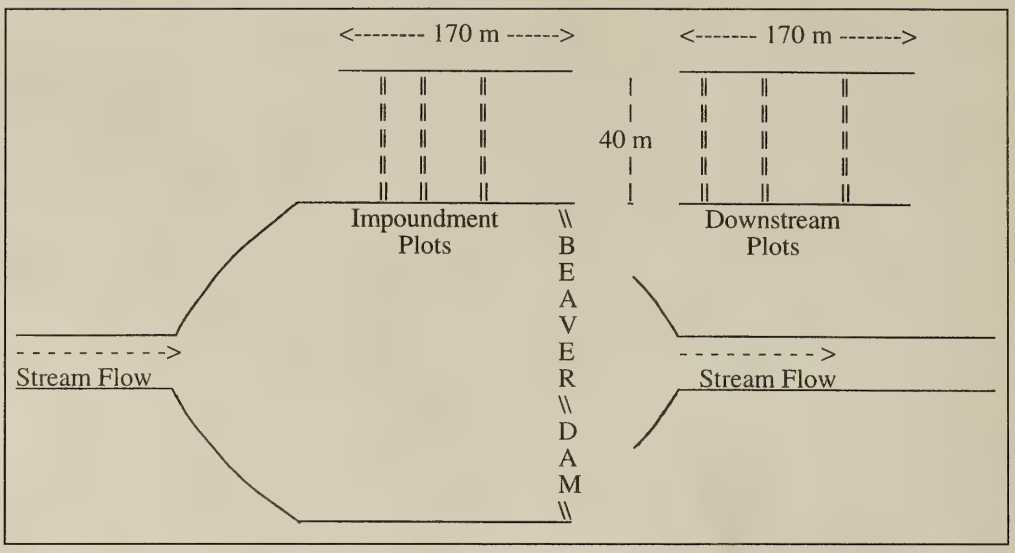

FIGURE 2. Sampling design for studying the impact of Beaver herbivory on shrubs and trees at eight recently active (< 5 years of occupancy), seven recently abandoned (< 12 years since abandonment), and eight old abandoned (> 12 years since abandonment) impoundments and the downstream comparison plots in the Swanson River basin of the Chapleau Crown Game Preserve, 1993.

number (combining all the transects) were used to determine Beaver herbivory. No data was collected at recent and old abandoned impoundment sites, because the decayed state of cut stumps made species identification unreliable.

To assess the recovery of shoreline woody plants after Beaver herbivory, we established sample plots along the shoreline of the seven recently and eight old abandoned impoundments. For comparison, we chose vegetation plots downstream of these abandoned impoundments. These plots were established where the stream returned to its original width (Figure 2). A straight-line measurement was taken from mid-dam to the impoundment shoreline. Using this distance, we were able to offset the downstream plot location away from the water's edge, thus ensuring the sampling of a similar forest sector as that of the impoundment plot (Figure 2). Employing the same methodology used for recently active impoundments, we recorded shrub and tree diameters and later calculated their basal areas and density. To evaluate differences among woody plant basal areas and density associated with recently abandoned and old abandoned impoundments and their respective downstream comparison plots, we performed a split-split-plot analysis of variance followed by Least Significant Differences Tests (Velleman 1992).

At each of the recently abandoned and old abandoned impoundments and their respective downstream control sites, we measured the changes in the woody plant community using three ecological indices; species richness, diversity, and evenness. Species richness of shoreline woody vegetation was determined by a direct count of the number of species within the sampling plots (Ludwig and Reynolds 1988).

Although most ecologists have used the Shannon's Index, i.e. - $[\Sigma(n_i/n)/Ln(n_i/n)]$ where n_i = *i*th of S species in the sample *and*

n = total number of individuals in the sample,

to determine species diversity, this estimator is biased, as the total number of species found within a community will most likely be greater than the number of species observed in any sample (Ludwig and Reynolds 1988). To overcome this bias, Hill's Diversity Number 1: $N1 = e^{-[\text{Shannon's Index}]}$ (Hill 1973; DeJong 1975) was used to measure species diversity.

There have been several indices developed to measure species evenness. In each case, if all species in a sample are equally abundant, then the evenness index should have a maximum value. Conversely, lower values mean a divergence away from evenness, i.e. dominance. Based on Ludwig and Reynolds (1988), we used Evenness Index 5:

$E5 = N2\text{-}1/N1\text{-}1.$

where N1 = Hill's Diversity Number 1 and N2 = Hill's Diversity Number 2,

N2 = 1/Simpson's Index, where Simpson's Index = $\Sigma(n_i(n_i\text{-}1)/ n(n\text{-}1)$,

n_i = *i*th of S species in the sample *and*

n = total number of individuals in the sample.

E5 values approach zero when species become dominant and one when evenness is a maximum (Alatalo 1981).

Once again, to evaluate differences among ecological indices associated with recently abandoned and old abandoned impoundments and their respective downstream vegetation plots, we performed a split-

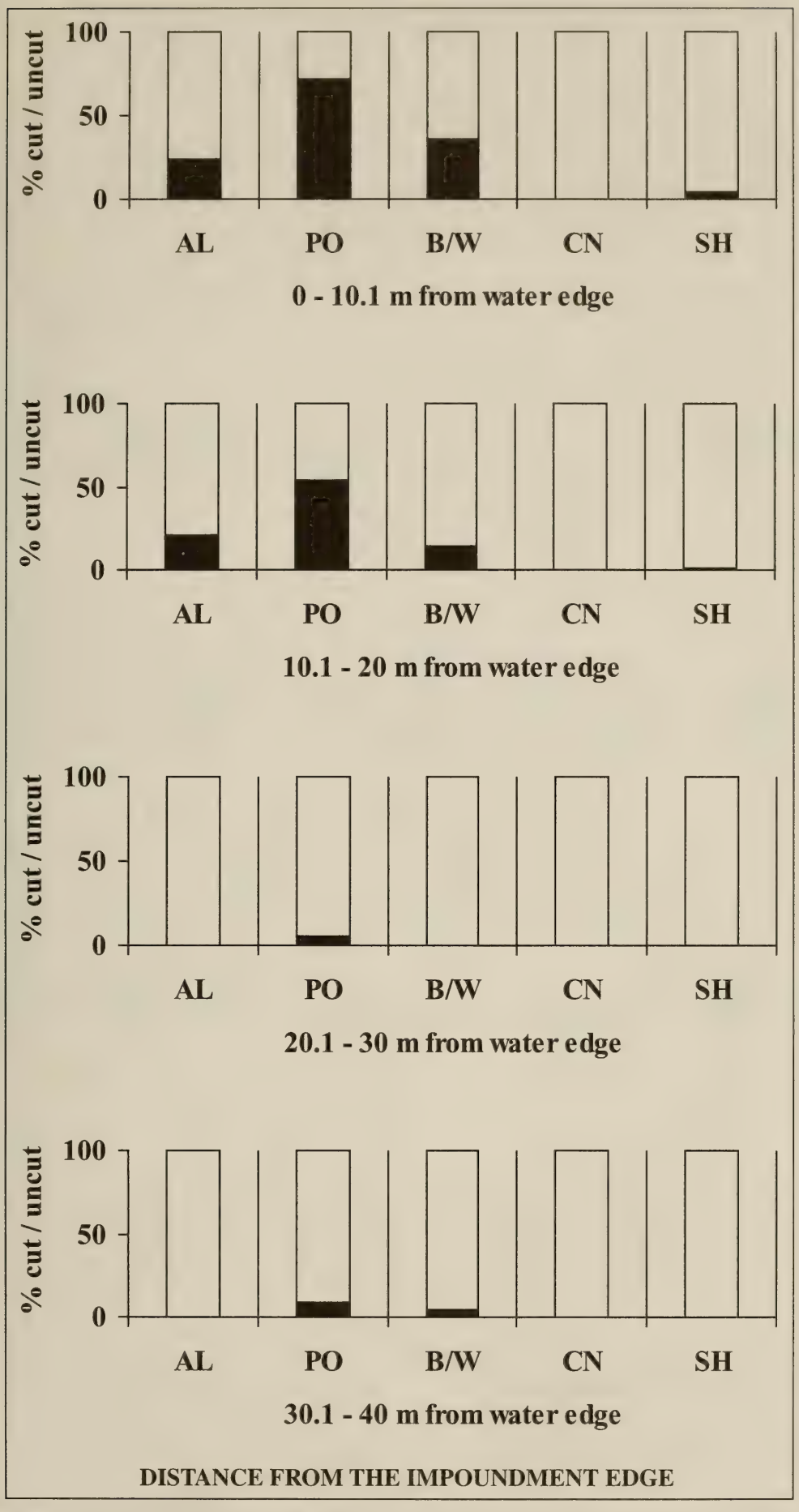

Figure 3. Proportion of Beaver cut ■ and uncut □ woody plants at 10 m intervals within 40 m of the impoundment edge of eight recently active dams (< 5 years of occupancy) in the Chapleau Crown Game Preserve, 1993.

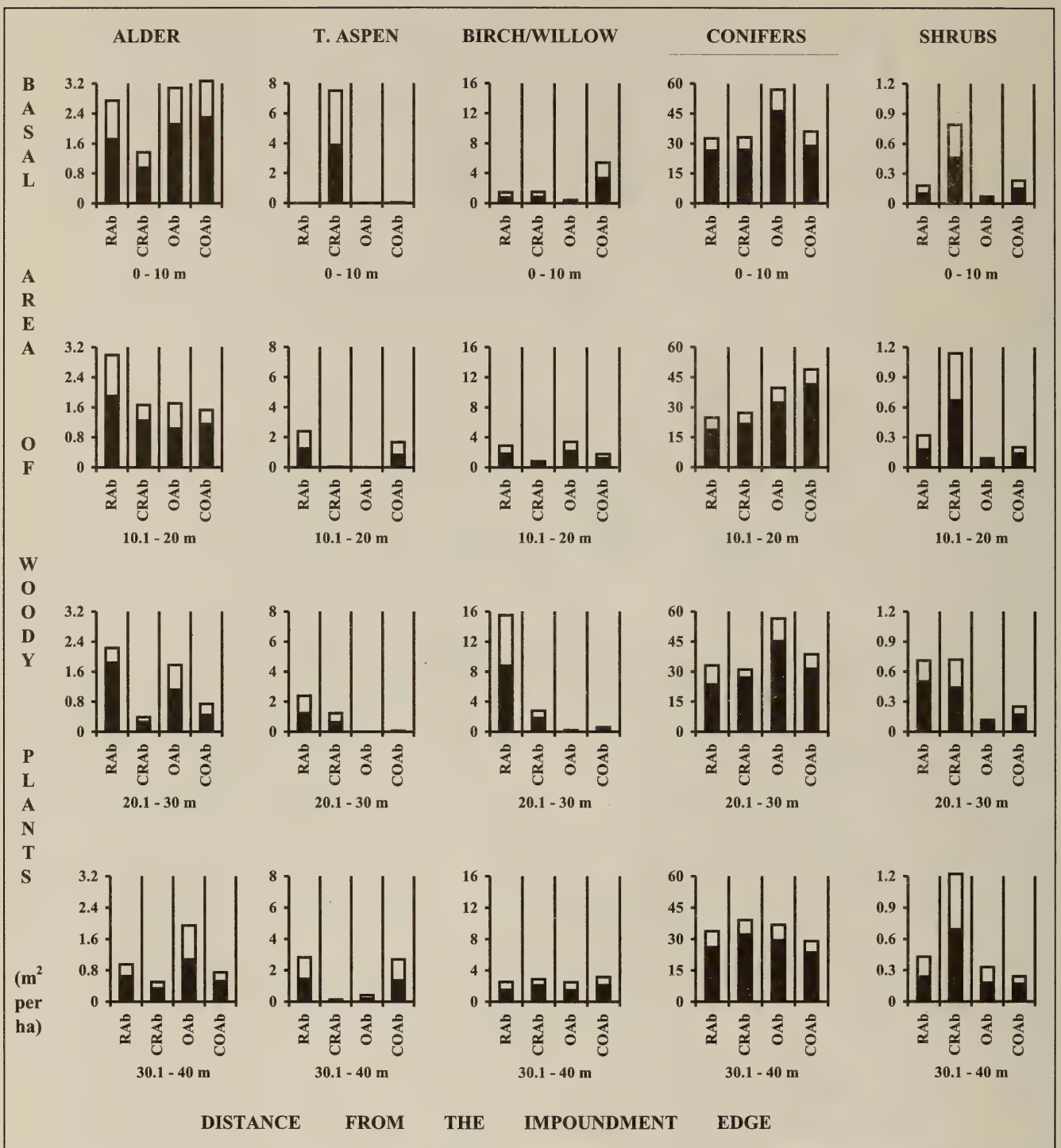

FIGURE 4. The basal area (m^2/ha) ■ and SE □ of woody plants at 10 m intervals within 40 m of the impounded edge of seven recently abandoned (RAb, < 12 years since abandonment), and eight old abandoned (OAb, > 12 years since abandonment) impoundments and the downstream comparison plots in the Swanson River basin of the Chapleau Crown Game Preserve, 1993.

split-plot analysis of variance followed by Least Significant Differences Tests (Velleman 1992).

We determined the power of our 2 × 2 × 4 split-split-plot factorial ANOVA by the using a Table of Minimal Detectable Differences Δ, for a fixed factor or interaction in a general design, a = 0.05, b = 0.10 (Appendix 12 – Lorenzen and Anderson 1993). If Δ is less than 0.5, then the experiment is capable of detecting extremely small differences among the factor levels. If D is between 0.5 and 1.5, then the experiment is capable of detecting small differences among the factors.

Results

Herbivory at Recently Active Beaver Impoundments

Beavers concentrated their cutting activity within 20 m of the shoreline of the recently active impoundments, 12% of available stems (41 cut, 390 avail-

able) within 10 m of the impoundment edge and 9% between 10.1 – 20 m (Figure 3). At distances 20.1 – 30 m and 30.1 – 40 m, Beavers only harvested 0.4% (4 cut, 493 available) and 1% (3 cut, 247 available) of available stems (Figure 3). In addition, we found 49 % of all cut stems within 10 m of shore and 91% within 20.1 m (Figure 3).

More specifically, Beavers concentrated their foraging for food items in close proximity to water. Within 10 m of the water's edge 71% (5 cut, 7 available) of Trembling Aspen stems were harvested and 54% (7 cut, 13 available) at distances between 10.1 and 20 m (Figure 3). Only 7% (3 cut, 41 available) of Trembling Aspen plants were cut at a distance greater than 20 m (Figure 3). The forage of secondary food trees showed a similar pattern; at distances 0 – 10 m and 10.1 – 20 m, Beavers cut 36% (5 cut, 14 available) and 14% (4 cut, 28 available) of White Birch and Willow stems, respectively (Figure 3), and at distances 20 – 40 m, only 3% (1 cut, 34 available).

All Alder stems cut were within 20 m of impoundment edges, despite a similar number of available stems at 0 – 20 m (80) and 20.1 – 40 m (83) (Figure 3). The Beaver's cutting pattern did not vary greatly throughout the first 20 m, i.e. 24% (11 cut, 46 available) at distances between 0 – 10 m and 21% (7 cut, 34 available) between 10.1 – 20 m.

Beavers only foraged for other hardwood shrub species within 20 m of water; 4% (1 cut, 23 available) between 0 – 10 m and 2% (1 cut, 61available) between 10.1 – 20 m. This result occurred despite shrub densities being 1.6 times greater at distances greater than 20 m from water. No conifers were cut even though they were readily available throughout the plot width (164 available between 0 – 20 m and 197 between 20.1 – 40 m) (Figure 3).

Woody Plant Recovery at Abandoned Impoundments

Power Analysis. Using the technique developed by Lorenzen and Anderson (1993), we found that the power of our experimental design was appropriate. All three factors involved in the experiment had Minimal Detectable Difference Δ values of less than 0.5 and therefore capable of detecting extremely small differences (i.e. Condition – 0.47; Type – 0.47; Distance – 0.43). The experiment's factor interactions had Δ values of between 0.5 and 1.5, indicating the ability to detect small differences (Condition * Type – 0.67; Condition * Distance – 0.61; Type * Distance – 0.61; Condition * Type * Distance – 0.87).

Basal Areas. At both recently and old abandoned impoundments, we noted that the basal area of Alder and White Birch/Willow stems were not significantly different from basal areas found in the down-

TABLE 1. The significant results of a Split-Split-Plot Analysis of Variance of woody plant basal area (m^2/ha) found within 40 m of the shoreline of recently abandoned (RAb, < 12 years), and old abandoned (OAb, > 12 years) impoundments (Impd) and their respective downstream (DStr) plots in the Chapleau Crown Game Preserve.

Woody Plant Categories[1]	Main Effects	*P*	Interaction Effects	*P*	Least Square Differences (LSD)	*P*
Alder	Dist[2]	0.03			0–10 vs 20.1–30 m	0.06
					0–10 vs 30.1–40 m	0.01
					10.1–20 vs 30.1–40 m	0.02
Trembling Aspen			Cond[3] * Type[4] *Dist	0.008	RAb/Impd/ 0–10 m vs RAb/DStr / 0–10 m	0.01
White Birch and Willow			Cond * Dist	0.003	RAb/ 0–10 m vs RAb/20.1–30 m	0.002
					RAb/10.1–20 m vs RAb/20.1–30 m	0.005
					RAb/20.1–30 m vs OAb/20.1–30 m	0.0004
					OAb/10.1–20 m vs OAb/20.1–30 m	0.04
Conifer	No significance noted amongst the Factors and their Interactions					
Shrubs	Type	0.03				
			Type * Dist	0.05	Impd/ 0–10 m vs DStr/ 0–10 m	0.01
					Impd/10.1–20 m vs DStr/ 10.1–20 m	0.002
					Impd/30.1–40 m vs DStr/ 30.1–40 m	0.01
					Impd/ 0–10 m vs Impd/20.1–30 m	0.0008
					Impd/20.1- 30 m vs Impd/30.1–40 m	0.03

[1]Transformations with normal probability plots (Velleman 1992).
[2]Dist — Distance indicates where the sample area is located in relation to the impoundment's shoreline.
[3]Cond — Condition indicates whether the sample area is associated with a recently abandoned or old abandoned impoundment.
[4]Type indicates whether the sample area is associated with an impoundment or a downstream site.

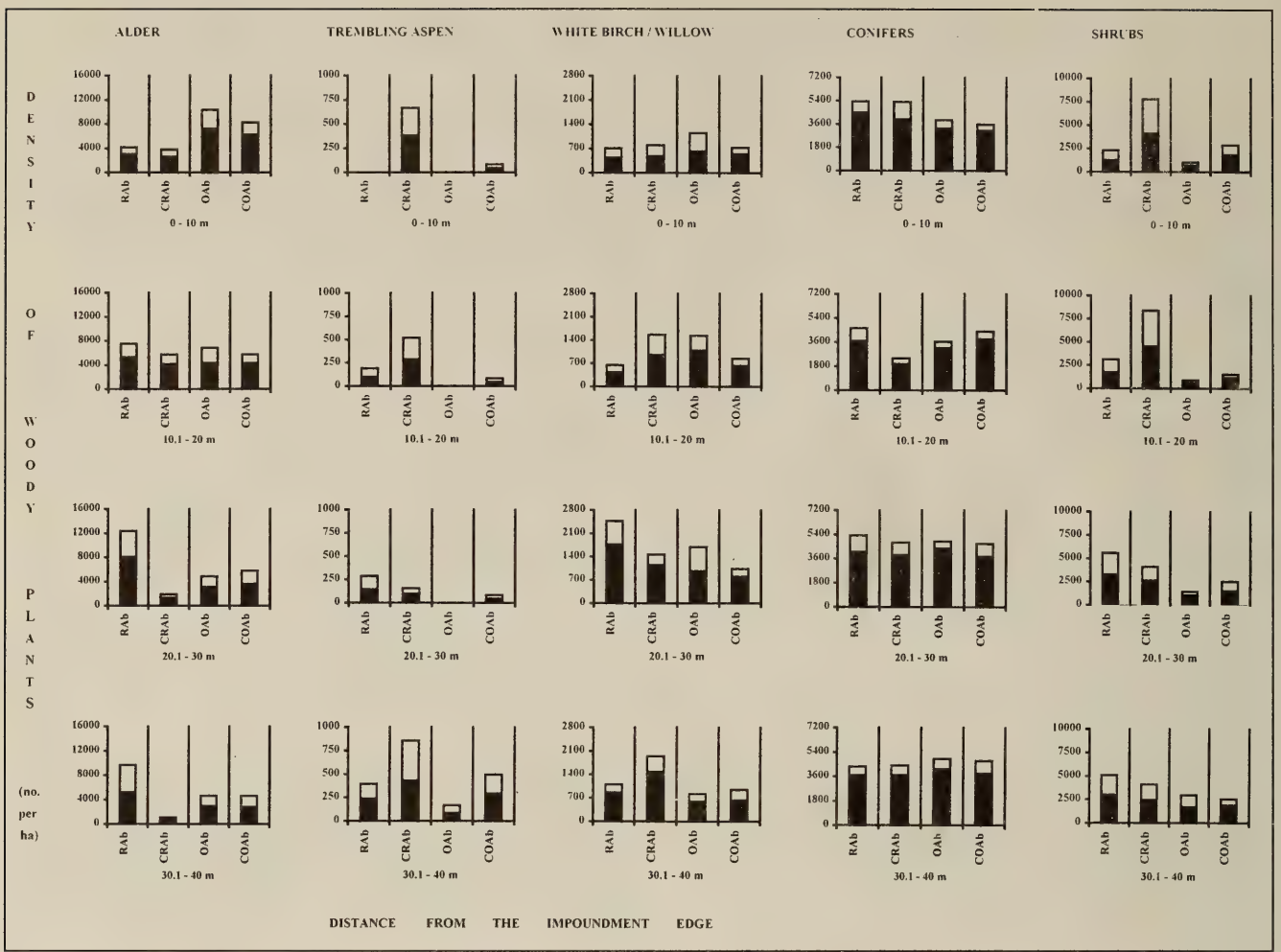

FIGURE 5. The density (number of stems/ha) ■ and SE □ of woody plants at 10 m intervals within 40 m of the impounded edge of seven recently abandoned (RAb, < 12 years since abandonment), and eight old abandoned (OAb, > 12 years since abandonment) impoundments and the downstream comparison plots in the Swanson River basin of the Chapleau Crown Game Preserve, 1993.

stream comparison sites (Figure 4 and Table 1). Alder and White Birch/Willow woody plants showed a general recovery to original levels.

Within 10 m of the recently abandoned impoundment shoreline, we found Trembling Aspen basal area was significantly less than their downstream comparison plot, indicating that these plants did not recover from Beaver herbivory. Between 10.1 and 40 m from shore, there were no significant differences. At old abandoned dam sites, we could not find evidence of Trembling Aspen within 30 m of shore (Figure 4 and Table 1).

At recently abandoned impoundments, we found that there was no significant difference in the basal area of conifers when compared to downstream comparison sites. At old impoundments, although conifer basal areas did not show any significant differences, on average there was a 60% increase in their basal area within 10 m of shore, 44% increase between 20.1 - 30 m, and 25% between 30.1 - 40 m (Figure 4 and Table 1).

At abandoned sites (recently or old), the basal areas of shrubs were significantly reduced at 0 – 10 m, 10.1 – 20 m, and 30.1 – 40 m when compared to their corresponding downstream sites. Shrubs, then, did not recover to original basal area values.

Density. At both recently and old abandoned impoundments, Alder and White Birch/Willow stems were not significantly different from the downstream comparsion sites, indicating that Alder and White Birch/Willow plants recovered to their original densities (Figure 5 and Table 2).

At recently abandoned dam sites, we recorded a significant decrease in Trembling Aspen density within 20 m of shore. In addition, when we compared the density within 10 m of shore with those at 30.1 – 40 m, we noted a significant increase in Trembling Aspen stems (Figure 5 and Table 2). At old abandoned sites, we did not detect the presence of any Trembling Aspen. Even at distances 30.1 - 40 m from shore, we discovered that the density was significantly reduced (Figure 5 and Table 2).

There was no significant difference found in conifer densities at recently and old abandoned dam sites (Figure 5 and Table 2). Generally, at both the recently and old abandoned dams, the density of

shrubs was found to be significantly less than original densities recorded in the downstream plots (Figure 5 and Table 2).

Ecological Indices. We found that there was no significant change in species richness, diversity, and evenness within 40 m of either recently and old abandoned impoundments when compared to their downstream sites (Figure 6).

Discussion

Herbivory at Recently Active Beaver Impoundments

Within the Swanson River watershed of the Chapleau Crown Game Preserve, we found that most of the foraging by Beavers was within 20 m of the impoundment edge. This narrowing of the Beaver's foraging range is interesting, considering they have the ability to haul stems 200 m overland (Novak 1987). We present three possible explanations for this phenomenon.

Our first explanation is based on thermoregulation in Beavers. Belovsky (1984) working on Isle Royale showed that Beaver summer activity was limited to only 4.5 hours, the peak being in the evening/night and secondary peak in early afternoon. Part of the explanation for this reduced feeding time was the thermal stress. The Beaver is a very clumsy and slow moving animal and as a result expends a lot of energy moving cut stems overland. Belovsky (1984) and Fryxell (personal communication) found no cut stems larger than 2.5 and 4.2 cm diameter, respectively, could be hauled intact by Beavers. Therefore, acquisition of a forage tree requires that the Beaver cuts down the tree, cuts it up into stems of manageable size, and then hauls it to the impoundment edge. Steen (1965), Miller (1967), and Coles (1969, 1970) concluded that the tail of the Beaver had an important function as an organ for controlled heat dissipation. Thus, Beavers may have chosen to forage close to water to facilitate tail wetting and control against hyperthermic increase in body temperature.

A second reason why Beavers may be cutting forage trees, (i.e. Trembling Aspen, White Birch and Willow) in close proximity to water may be due to how these trees grow in a riparian setting. Because

TABLE 2. The significant results of a Split-Split-Plot Analysis of Variance of woody plant density (number of stems/ha) found within 40 m of the shoreline of recently abandoned (RAb, < 12 years), and old abandoned (OAb, > 12 years) impoundments (Impd) and their respective downstream (DStr) plots in the Chapleau Crown Game Preserve.

Woody Plant Categories[1]	Main Effects	*P*	Interaction Effects	*P*	Least Square Differences (LSD)	*P*
Alder	Dist[2]	0.02			0–10 vs 30.1–40 m	0.003
					10.1–20 vs 30.1–40 m	0.01
Trembling			Cond[3] * Type[4] *Dist	0.05	RAb/Impd/ 0–10 m vs	
					RAb/DStr / 0–10 m	0.0004
Aspen					RAb/Impd/10.1–20 m vs	
					RAb/DStr /10.1–20 m	0.07
					RAb/Impd/30.1–40 m vs	
					RAb/DStr /30.1–40 m	0.01
					RAb/Impd/ 0–10 m vs	
					RAb/Impd/30.1–40 m	0.003
White Birch and Willow	Dist	0.02			0–10 vs 20.1–30 m	0.005
					10.1–20 vs 20.1–30 m	0.03
					0–10 vs 30.1–40 m	0.04
			Cond * Dist	0.02	RAb/ 0–10 m vs	
					RAb/20.1–30 m	0.0009
					RAb/10.1–20 m vs	
					RAb/20.1–30 m	0.002
					RAb/ 0– 10 m vs	
					RAb/30.1–40 m	0.006
Conifer	No significance noted amongst the Factors and their Interactions					
Shrubs	Type	0.02				

[1]Transformations with normal probability plots (Velleman 1992).
[2]Dist — Distance indicates where the sample area is located in relation to the impoundment's shoreline.
[3]Cond — Condition indicates whether the sample area is associated with a recently abandoned or old abandoned impoundment.
[4]Type indicates whether the sample area is associated with an impoundment or a downstream site.

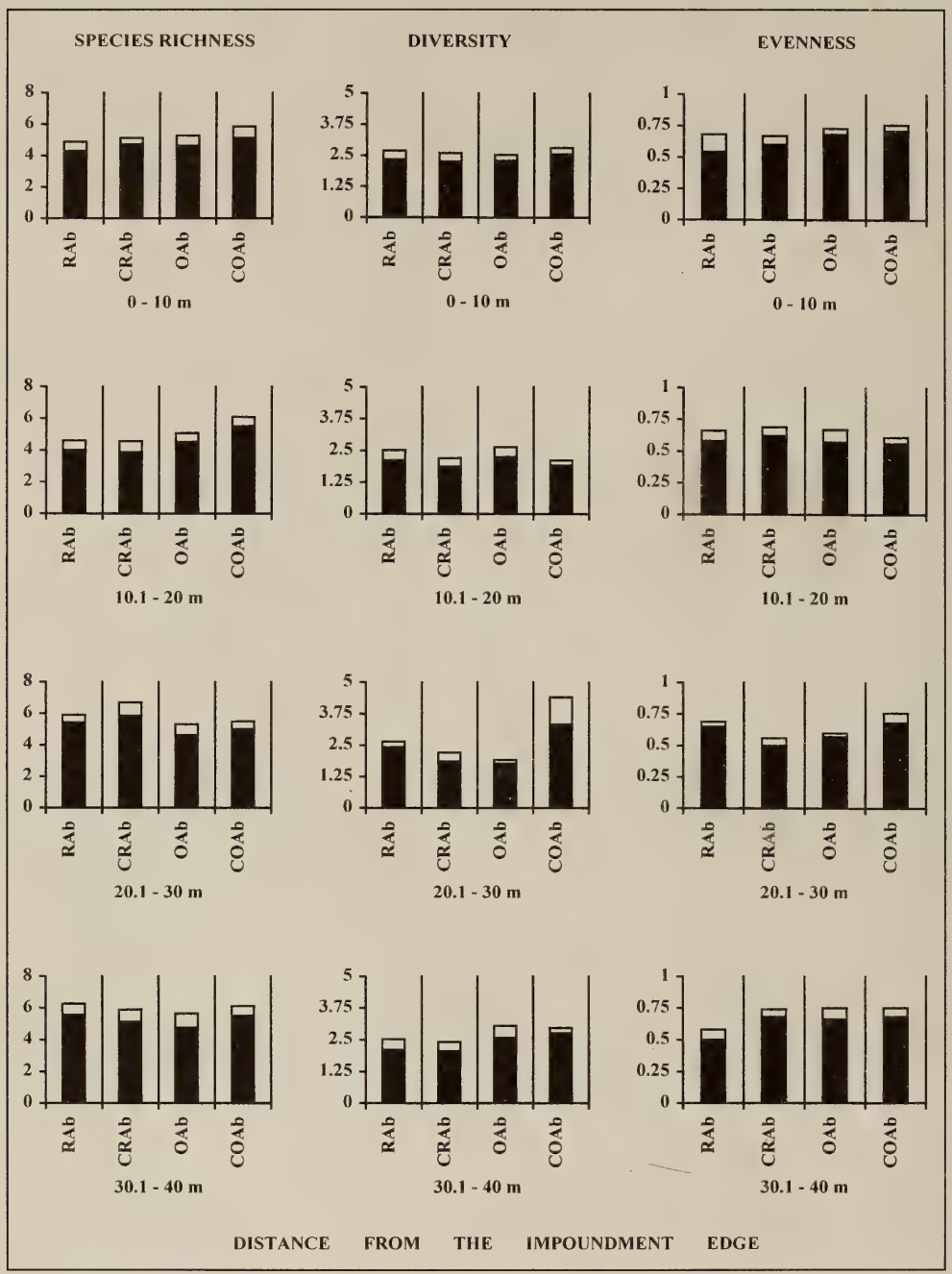

FIGURE 6. Species richness, diversity, and evenness index values ■ and SE □ for the woody plants at 10 m intervals within 40 m of the impounded edge of recently abandoned (RAb, < 12 years since abandonment), and eight old abandoned OAb, > 12 years since abandonment) impoundments and the downstream comparison plots in the Swanson River basin of the Chapleau Crown Game Preserve, 1993.

of reduced canopy and more sunlight, riparian trees tend to lean towards the water or have more foliage in that direction (Johnson 1983). Since Beavers cannot directionally fall trees (Novak 1976), we propose that Beavers over evolutionary time may have selected to cut trees close to the water as they are more apt to fall towards or into the water because of this disproportionate growth on their stream side.

The third reason involves the risk of predation. The trade-off between foraging activity and predator risk has long been regarded as one of the great ecological conflicts experienced by animals (Milinski and Heller 1978; Abrams 1984; Werner and Gillian 1984; McNamara and Houston 1987; Lima and Dill 1990; Anholt and Werner 1995; Werner and Anholt 1996; Eklov and Halvarsson 2000). The importance of predation during evolutionary time is clear, but growing evidence suggests that animals also have the ability to assess and behaviourally influence their risk of being preyed upon in ecological time (i.e., during their lifetime) (Lima and Dill 1990).

Beavers are classed as central-place foragers and as such move out from a central location to select food that may be eaten immediately or transported back to the central location for later use (Basey and Jenkins 1995). Researchers have long suggested that the Beaver's foraging behaviour has been affected by the risk of predation (Jenkins 1980; Belovsky 1984). Recently, Basey and Jenkins (1995) showed experimentally that Beavers were "trading off maximization of profitability against minimization of predation" by Coyotes (*Canis latrans*). Since Timber Wolves (*Canis lupus*) are very effective predators of Beavers (Pimlott et al. 1969; Frenzel 1974; Voigt et al. 1976; Theberge et al. 1978; Potvin et al. 1992) and commonly prey on Beavers within our study area (Carbyn 1987; MacDonell 1993; Elliott 1997), we suggest that these northern Beavers may be adjusting their foraging patterns to minimize capture by large predators such as Timber Wolves.

To date, there have been no field studies that demonstrate experimentally that Beavers reduce their foraging range in response to predator pressure. However, we believe some evidence of this predator-induced reduction trend can be seen when we compare Beaver foraging studies done in areas where Timber Wolf populations are high with those without these large predators. On Isle Royale, in northern Minnesota, and southern Algonquin Provincial Park, areas known to have high Wolf population levels, studies by Belovsky (1984), Johnston and Naiman (1990) and Donkor and Fryxell (1999, 2000), have documented Beaver feeding activity is largely concentrated within 20 m of water. In contrast to this, Beaver studies done in Maine (Hodgdon and Hunt 1953) and Michigan (Bradt 1947), areas where no Timber Wolves reside, show that the foraging range is greatly expanded.

Alder plays a crucial role in minimizing predation by Timber Wolves. Across the northern landscape, the ubiquity of streamside Alder provides Beavers with a ready source of preferred dam-building material in close proximity of the water's edge (Barnes and Mallik 1996). Since Beavers are able to transport whole Alder stems overland with no appreciable energy cost (Barnes and Mallik 1996), they are able to construct dams with high efficiency. Beavers within our study area did not have to venture further than 20 m to obtain Alder stems (Figure 3). This situation ensures the speedy establishment and maintenance of a dam, thus providing a protective water environment against predation.

Woody Plant Recovery at Abandoned Impoundments

Donkor and Fryxell (1999, 2000) found that Beavers had a great effect on species richness and diversity three years after a dam site was abandoned. Our findings are contradictory. We found that there were no significant changes in these two ecological indices over an extended period of time (12+ years). A possible explanation for this discrepancy could be found in their choice of sample size. In their study, Donkor and Fryxell (1999, 2000) used one abandoned site. We found that there was much variation from one site to another and found it necessary to use 15 sites to account for these fluctuations in measurements.

Over time, we found that the Trembling Aspen did not show any signs of recovery. Indeed, their presence after 12 years was not detected by our sampling techniques. Since we had no details concerning the colonization history of these dam sites, Beavers may have occupied these sites several times in the intervening years and their harvesting pressure may be spread over the time period, not giving Trembling Aspen enough time to recover. Similarly, Gese and Shadle (1943) and Graham et al. (1963) found that regeneration of Trembling Aspen was greatly hampered by the continual cutting by herbivores, such as Beavers and White-tailed Deer (*Odocoileus virginianus*).

Johnston and Naiman (1990) showed that Beaver herbivory is especially significant in the boreal forest, because it affects the overstory causing increases in light, temperature, and nutrients. In our study, we found that after 12 years of abandonment, there was an increase in the basal area of conifers adjacent to abandoned Beaver impoundments. Lawrence (1952) working in Michigan found that after 10 years of abandonment, there was a substantial increase in the growth of shoreline conifers. Based on their work in northern Minnesota, Naiman et al. (1988) and Johnston and Naiman (1990) noted that selective cutting by Beavers could cause a shift towards conifer-dominated forests. Bryant and Chapin (1986) and Pastor et al. (1988) showed that selective browsing by other forest herbivores had a similar result.

Slough and Sadleir (1977) believed that Trembling Aspen was an important factor in maintaining healthy Beaver populations in northern Canada. Since the Trembling Aspen is an early seral stage plant, fire is needed to open up new colonization areas (Graham et al. 1963). Because of this Slough and Sadleir (1977) proposed using fire as a silvicultural tool to increase high quality Beaver forage. At that time, the use of fire was not widely practiced (Slough and Sadleir 1977). Fire, however, is now considered one of the most significant disturbances in northern forests. In recognition of its importance, the Ontario Ministry of Natural Resources has recently produced draft forest management guidelines for retaining forest ecosystem structure and function using fire disturbance patterns as a template (Anonymous 2000).

We believe that as more of these novel, more ecologically sensitive, forest management strategies are implemented across the forest landscape, disturbance-reliant species such as the Beaver will flourish.

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Comparison of Parental Roles in Male and Female Red Foxes, *Vulpes vulpes*, in Southern Ontario

VALERIA VERGARA

Trent University, Biology Department, Peterborough, Ontario K9J 7B8, Canada
Present address: Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada

Vergara, Valeria. 2000. Comparison of parental roles in male and female Red Foxes, *Vulpes vulpes*, in southern Ontario. Canadian Field-Naturalist 115(1): 22–33.

The Red Fox (*Vulpes vulpes*) is normally monogamous but often deviates to polygyny. Variability in paternal behaviour may be just one part of its general social system flexibility. I evaluated the extent of male participation in parental care in eight Red Fox families in one suburban and seven rural habitats of southern Ontario, by examining the relative contribution of males and females in rearing the young. I observed a wide range of strategies and considerable variation amongst males' involvement in raising the kits. The observed variation occurred within a relatively small geographical area and, except for an urban den, the den sites were in similar rural habitats. Despite this variability, several behavioral patterns emerged. Females visited the den more frequently and for longer periods of time than males, they spent a greater proportion of time in behaviors that indicate parental attentiveness (excluding nursing), and they stayed closer to the young. Males spent significantly more time than females in vigilant behaviour.

Key Words: Red Fox, *Vulpes vulpes*, parental care, paternal care, monogamy, helpers, Ontario.

The most common mating system among canids is "obligate monogamy" (Kleiman 1977). Correspondingly, some form of male care is widespread in canids (Malcom 1985). Male care has been observed in over half (21/36) of the species in the family Canidae (Malcom 1985; Asa and Valdespino 1998). Data on the rest of the canid species are not available.

Several studies of parental behaviour in canids have documented the distribution of care-giving behaviour between the sexes (Wolves, *Canis lupus*: Harrington and Mech 1982, Fentress and Ryon 1982; Jackals, *Canis mesomelas* and *canis aureus*: Moehlman 1983; Red Foxes: Macdonald 1979; African Wild Dogs, *Lycaon pictus*: Malcom and Marten 1982; Maned Wolves, *Chrysocyon brachyurus*: Rasmussen and Tilson 1984; for a review see Malcom 1985). An examination of such studies reveals a substantial amount of interspecific variation within the family in terms of the contribution of the male to raising the young. In some species the male feeds the young as much as the female (e.g., Arctic Foxes, *Alopex lagopus*: Garrott 1980; jackals: Moehlman 1986) and in others there is no indication that the male provides food either to the female or to the cubs (e.g., Blanford's fox, *Vulpes cana*: Geffen and MacDonald 1992; Maned Wolf: Veado 1998; see Asa and Valdespino 1998, for review of canid reproductive biology).

In order to identify the subtle reasons for changes in the reproductive strategies of canid species, it is important to quantify parental care. Any such attempts should compare actual amounts of paternal and maternal care, and investigate how male care varies among years and between different populations or individuals of a particular species. The Red Fox (*Vulpes vulpes*) is remarkably well suited for this type of study. It has the largest geographical range of any living carnivore (Henry 1993), and its social system is exceptionally flexible.

Pronounced differences in the behaviour of Red Foxes between urban, rural, suburban, agricultural, and woodland habitats have been reported (e.g., Macdonald 1980; Doncaster and Macdonald 1991; Voigt and Macdonald 1984; Voigt 1987; see Cavallini 1997 for review). While monogamous pairs seem to be the norm in some habitats (Storm et al. 1976; Voigt 1987) other habitats sustain cooperative groups where polygyny (Macdonald 1979) and polyandry (Baker et al. 1998) are common. Even in the same area in different years the same fox population may exhibit alternate social strategies in response to variations in food supply (von Schantz 1984; Henry 1986; Zabel and Taggart 1989).

Female foxes may tolerate a polygynous mating system where the male is not devoted to only one female and her young, provided that the costs of sharing the male's help may be outweighed by the advantage of mating with a superior male in a more suitable area (polygyny threshold model: Verner 1964; Orians 1969). Consequently, the contributions by each sex to parental care may be unequal. Trivers (1972) suggested that each sex attempts to maximize the care its mate provides while minimizing its own contribution. This study aims to understand how this inherent conflict between the sexes applies to potentially monogamous, but sometimes polygynous, Red Foxes. Some studies suggest that the male may supply the majority of food for the kits (Henry 1986;

Macdonald 1979), while others indicate that males share little of the responsibility of looking after the kits (Burchfield 1979). This variability in paternal behaviour may be just one part of a general social flexibility, or it could be simply a reflection of a lack of studies dealing specifically with the role of the male in the family group.

In this study I evaluate the extent of male participation in kit-rearing in eight Red Fox families in suburban and rural habitats of southern Ontario. Specifically, how do males contribute to rearing the young and how does this compare to the female's contribution in rearing the young?

Study Area and Methods

The study was conducted during April – June 1994 and 1995. Seven rural habitats and one suburban habitat of southern Ontario (all within a 90 km radius of the city of Peterborough) were included in the study (see Table 1). The area is characterized by warm summers and cool winters. Temperatures average, for a thirty year period, 16.6° C in June, 19.7° C in July, -9° C in January and -7.8° C in February. The 1994 study year was colder than normal both in January (-15.9°C) and February (-11.7° C), warmer than normal in June (18.0° C) and close to normal in July (19.8° C). The 1995 study year was warmer than

TABLE 1. Composition of the studied families, hours of observation and den characteristics.

Family	F	M	H	Litter Size[1]	Hours of Observation	Location	Den site Characteristics
Gaines	Y	Y	–	4	72	City of Coubourg 43°58' N, 78°10' W	Fenced field behind dog-food factory, suburban habitat, two distinct den areas 200 m apart simultaneously in use, multiple entrances.
Keene	Y	Y	Y	6	75	Otonabee Township 44°15' N, 78°08' W	Open field, 300 m from barn, rural habitat, two distinct den areas 110 m apart in use, multiple entrances.
Tweed	Y	Y[2]	–	7	88[3]	Huntingdon Township 44°28' N, 77°25' W	Fenced hay and alfalfa field, rural habitat, two distinct den areas 60 m apart in use, multiple entrances.
Douro	Y	Y	–	6	105	Douro Township 44°23' N, 78°12' W	Open hay field, 300 m from farm house, rural habitat, multiple entrances.
Railway	Y	Y	–	4	139	Seymour Township 44°17' N, 77°50' W	Open grassy hill side, 100 m from old railway track, rural habitat, two distinct den areas 50 m apart simultaneously in use, multiple entrances.
Pogue	Y	Y	-	9	131	Verulam Township 44°33' N, 78°40' W	Open hay field, 50 m from farm house, rural habitat, multiple entrances.
Knox	Y	Y	Y	5	76	Otonabee Township 44°18' N, 78°14' W	Open grassy hill side, rural habitat, four distinct den areas 30 m apart in use.
Highway	Y	–	–	2	38[4]	Otonabee Township 44°15' N, 78°09'	Fenced grass field, rural habitat, two den areas 27 m apart simultaneously in use, multiple entrances, one den only 2 m from Highway.

F = female; M = male; H = helper; Y = present. [1]Number of kits in each family at the beginning of the observation period. [2]The Tweed male was only present until the kits were seven weeks old. [3]44 out of the 88 hours were observations made from blinds by John and Janet Foster (film makers and owners of the property) during the making of their documentary on Red Fox behavior, two weeks prior to my arrival to the study site. Their notes were kindly provided to me. [4]Observations at the highway family den were made in four sessions throughout a period of over one week. During this time I only saw two kits and the female. The male was never seen. I found the carcasses of two other kits lying at the side of the road; they had been killed by cars.

normal in January (-5.6° C) and colder in February (-9.9° C), warmer in June (18.3°C) and close to normal in July (19.5° C). Precipitation is rather uniform throughout the region and year varying from about 28 cm to 39 cm. The seven rural habitats in this study were typical of the southern Ontario landscape, with a mixture of cropland (principally hay and corn), uncultivated fields, cow pastures, and intermittent mixed forests of evergreen and deciduous trees.

My study was carried out on a total of eight different Red Fox families (four each season) located with the help of interested rural residents. All observations were made at the den sites, from a small vehicle, a tent, or a building. Since all eight den sites were in open areas, they could be observed from a distance of over 100 m with the aid of a spotting scope and wide-angle binoculars. At three of the den sites observations were made from a building, so the foxes could not see the observer (Gaines, Tweed, and Pogue dens). At the other five sites the foxes became habituated to the presence of the research vehicle or the tent within one to two days.

Each adult was identified by the pattern of black pigmentation on the muzzle, the extent of white on the chest and neck, the shade of the fur (ranging from a light, sandy colour to an intense orange), and the shape and extent of white on the tip of the tail. It also soon became possible to identify adult male and female foxes based on differences in their behaviours. In fact, gender identification by behavioural differences has also been reported in other observational natal den studies (Swift Fox, *Vulpes velox*: Pruss 1994).

In total, 724 hours of observations were conducted on the eight dens. A recorded hour is defined as an hour observing the den site, regardless of whether the adults were present or the kits were above or underground. Dens were observed primarily during hours of daylight, but did include 20 hours of nocturnal observations using an ambient light image-intensifier scope.

I adopted the working definition proposed by Woodroffe and Vincent (1994), and considered male care as any behaviour that benefits the young and that the male would not carry out if young were not present. Such direct parental behaviour includes: visiting and providing food to the cubs, resting and huddling with them, grooming, carrying, retrieving, actively defending, babysitting, and playing or socializing with the kits. I also looked at one form of indirect care: vigilant behaviour, and at adult-young distances as a measure of attentiveness which has been used in previous studies (Walters 1984).

Instantaneous scan samples (see Altmann 1974) were taken at 30-second intervals. The percent of time is estimated from the percent of samples or intervals in which a given activity was recorded (Altmann 1974). This method of data collection can be used to obtain data from more than one group member, by observing each in turn. If the behaviour of all visible group members (in this case adults and kits) is sampled within a very short time period the record approaches a simultaneous sample on all individuals. Thus, this technique allowed to take full advantage of those instances in which the whole family unit was seen at once. Every 30 seconds, the activity of the adult and the kits and the distance of each adult to the nearest kit were recorded. I defined my behavioural categories based on observations made during den watching in a 1993 pilot study, and on the forms of direct care listed by Kleiman and Malcom (1981) and Woodroffe and Vincent (1994). Also, the number and duration of each adult visit to the den and the number of trips when an adult brought a prey item to the kits (and the type of prey) were noted.

For each family the number of visits to the den made by each adult was divided by the total number of hours of observation of that family. Thus, the frequency of visits per hour (visiting rates) was calculated for each adult.

To estimate the distances, I considered one adult fox body length to equate 1 m. This method was verified with the research assistants that were helping at three den sites (Gaines, Keene and Railway), by practicing estimating a few distances between chosen features of the terrain, and then measuring the actual distances to confirm that they fell within the estimates.

Families studied and times of observation

I conducted my observations from the time the kits were 5 weeks of age (kits emerge from the den at about 4 weeks), until approximately 11 weeks of age (see Figure 1). The composition and location of each family and the total number of hours of observation at each den-site are summarized in Table 1 (further details on each family are given in Vergara 1996). The end of my observations of each family

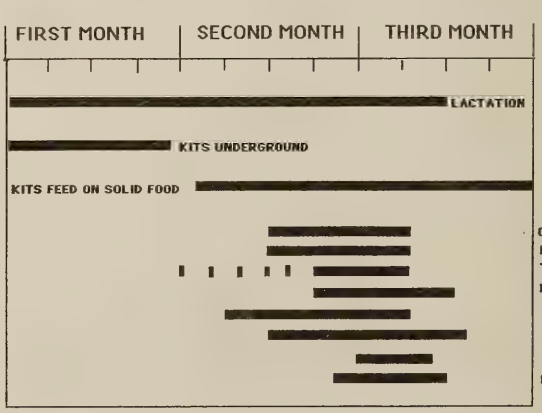

FIGURE 1. Observation times for each family in relation to the major events in the rearing cycle. Dashes (Tweed) indicate that the family was observed during that time period, but data were recorded in a different fashion (ad libitium).

was not arbitrary but triggered by the sudden move of the foxes to a new unknown or unobservable den. Figure 1 shows the times at which the different families were observed in relation to the general development of the cubs (diagram design borrowed from Malcom and Marten 1982).

The Highway den was only observed for 38 hours (four sessions, between 8 and 10 hours in duration each, distributed in one and a half weeks), and the male was never seen. The lack of male visitation at this den might be a reflection of the relatively low number of hours of observation of this family compared to the other families (average of 98 h). Similarly I observed the Tweed family for 44 hours (four 12-hour sessions distributed in two weeks), and obtained additional 44 hours of recorded observations (a total of 88 hours) by documentary makers John and Janet Foster (see Table 1). I never observed the male, but he visited the den three times during the 44 hours prior to my arrival (John and Janet Foster, personal communication). Thus, statements concerning male visitation rates and feeding rates throughout this paper will be based on the remaining six families.

Results

Visiting Rates

Any adult fox within 0 to 100 m from the den site was recorded as visiting the den. In general, adults visited during all hours of the day, but predominately in early morning (up to 3 hours after sunrise) and evening (2 or 3 hours before dusk). Although visits in the middle of the day were not infrequent, they were usually shorter in duration.

Figure 2 shows the frequency of visits per hour for each adult. A Mann-Whitney U test revealed significantly more visits/hour by females than males ($W = 84.0$ $p \leq 0.02$). Females averaged 0.2 visits per hour (S.E.= 0.03) and males averaged 0.1 visits per hour (S.E.= 0.027). There is no significant correlation between the visiting rates of males and females ($r = -0.041$, $df = 5$, $p > 0.05$).

Excluding the Tweed and Highway families, male visitation rates varied from 0.06 visits/hour at the Railway den, to 0.24 visits/hour at Gaines (the adult male in this family visited the kits more often than the female did).

Duration of the Visits

For each family, the total number of visits for which a duration was known was used to calculate the mean time/visit for each adult (Figure 3). Males usually made shorter visits than females. The overall weighted average for females was 45 minutes, and for males 22 minutes. Thus, females stayed, on average, twice as long as the males did when they visited the den. Yet, as shown by the standard errors, the visits varied considerably in length. The Railway female, for instance, stayed for a minimum of 4 minutes, and a maximum of 171 minutes.

Pupsitting by males

Dog foxes spent a large proportion of their time at the den site in the absence of the vixens (Figure 4). On average, 78 % of the time spent by males at the den site they were there alone (SE = 8.7 %). This is referred to as "pupsitting" or "den guarding" in other studies (e.g., Moehlman 1983, for Silverbacked and Golden Jackals; Malcom and Marten 1982, for African Wild Dogs; Pruss 1994, for Swift Fox).

Feeding the kits

Number of prey items per trip

The average number of prey items per trip was calculated by dividing the total number of prey items each parent brought to the young by the observed number of visits of that parent (Figure 5). There was no significant difference between males and females ($W = 55.0$ $P > 0.1$, Mann-Whitney U-test), however five of the six males have higher values than females, reflecting the fact that when males visited the den, they usually did bring food.

Relative feeding contributions

Figure 6 shows the relative contributions of each adult to feeding the kits in the two-parent families

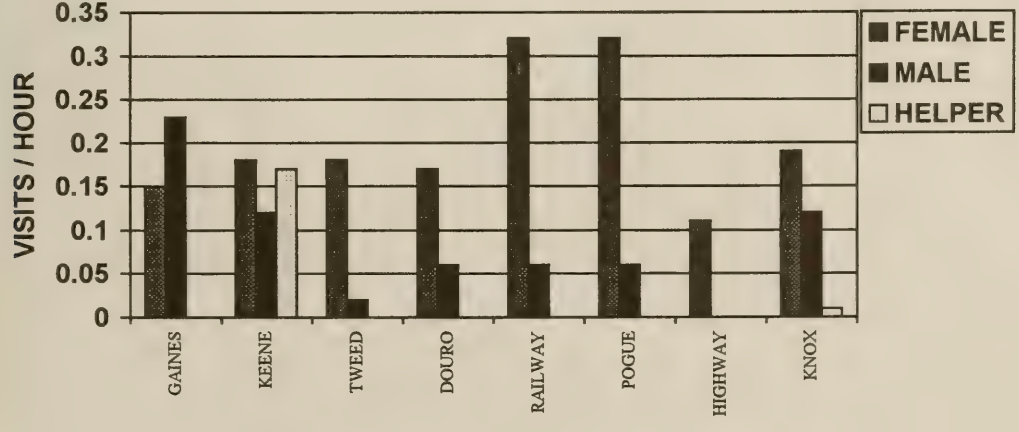

FIGURE 2. Frequency of visits/ hour by each adult in each family.

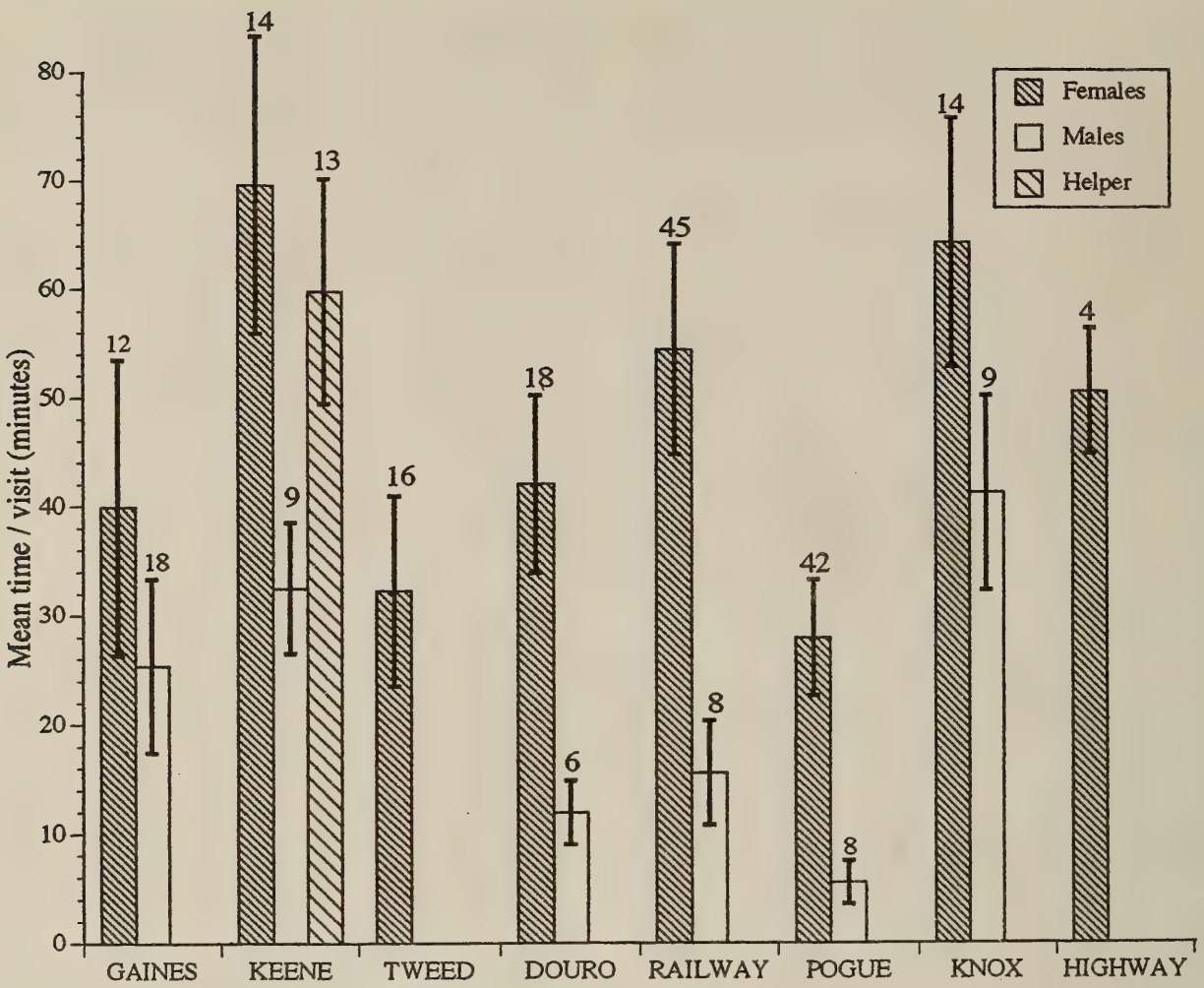

FIGURE 3. Mean duration of visits (in minutes) for adults in each family. Vertical bars represent standard errors. The numbers above each bar represent the total number of visits to the den by that individual. The means are based on the number of visits for which the actual duration was known.

(Highway and Tweed families: male absent during my observation period), as a proportion of the total number of prey items that the kits received. The Gaines and Knox males were the most attentive fathers, contributing 64 % and 46 % of the total number of food items respectively. The males of three families, Douro, Railway and Pogue, provided only 20 % of the food items. The third adult (a helper, see below) in the Keene family contributed 41 % of the total food items, more than the female or the male in the family (each provided 29 % of the food items).

Figure 7 shows the types of food items that males and females were observed to bring to the cubs. Small rodents constituted the bulk of the food items for both males and females. More groundhogs were brought to the den by males than females (13 % vs. 1 %). Only the Tweed vixen was observed bringing a groundhog to the kits.

Behavioral comparisons between males and females

Figure 8 shows the average proportion of time that males and females spent in different behaviours. Aside from nursing, the main difference between males and females seems to be in time spent in vigilant behaviour (females 35 %, males 60 %), and grooming the kits (females 12 %, males 2 %). Four of the six males groomed the young (Gaines, Keene, Douro and Knox), and did so a lower proportion of time than the respective females (Gaines: 1 % vs. 5 %; Keene: 4 % vs. 12 %; Douro: 4 % vs. 30%; Knox: 1% vs. 10 %). Vigilant behaviour was considered an indirect form of care, represented by two behavioural categories: casual scan and very alert scan. When these categories were combined into one, males spent a significantly higher proportion of time than females in such alert behaviour ($p \leq 0.02$, Mann-Whitney U-test).

The following behaviours were combined to provide a single value for parental attentiveness (excluding nursing) to test for significant differences between the sexes: (a) picking up and carrying prey items at the den site, caching them, dropping them at the den mound or feeding them directly to the kits; (b) grooming or cleaning the kits; (c) playing with the kits, (d)

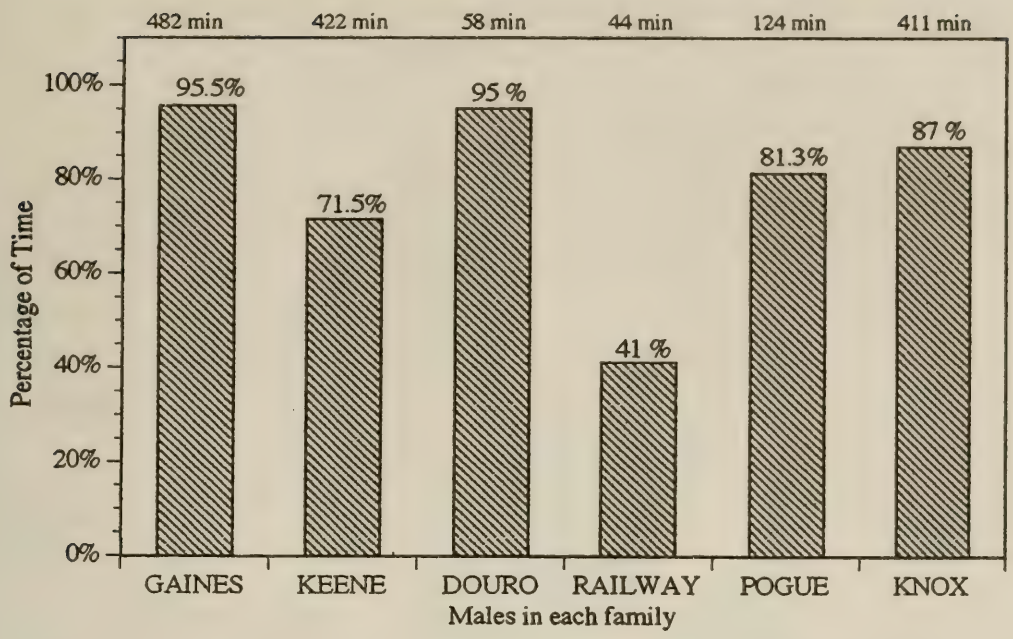

FIGURE 4. Percentage of the total time spent by males at the den site in the absence of the female. The 100 % level represents the total time (in minutes) that each male attended the den. The relatively small amounts of time for the Douro, Pogue, and Railway families reflect the fact that the visits of these males were particularly brief (usually to bring food to the den and leave).

making muzzle to muzzle contact with the kits, usually when the kits are soliciting food (i.e., "being solicited"); (e) being harassed or followed by the kits, which refers to all those instances when the adults passively tolerated kits that persisted in following the adult, biting its legs and tail, climbing over it, or pouncing on it; and (f) checking the den entrances, which refers to an adult sticking its head and upper body in a den (if the cubs are inside the den, this behaviour often summons them out). Overall, females spent a significantly greater proportion of time (27.6% on average) than males (16.1 % on average) in behaviours that indicate parental attentiveness (Mann-Whitney U-test, W = 78 $p \leq 0.02$).

Females interacted with the kits in their visits significantly more than males (chi square goodness of fit for two samples, $\chi^2 = 45.8$, df = 1, $P < 0.001$). Males often came to the den site bringing a food item without approaching the kits or interacting with them in any way (28 % of the visits were non-interactive, n = 59), dropping the item near the main den entrance and immediately moving away from the mound. Females interacted with the young in 96 % of their visits (n = 156).

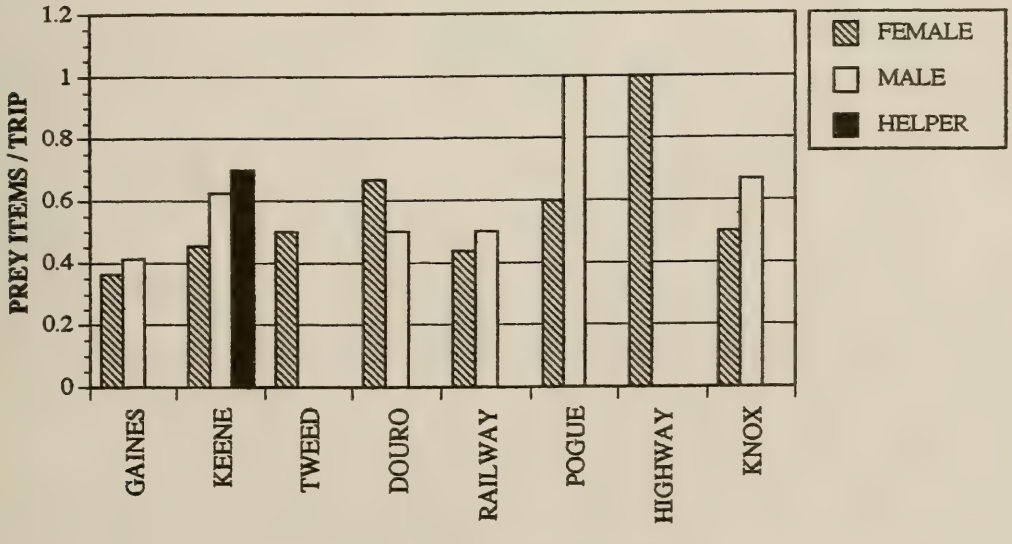

FIGURE 5. Number of prey items/visit for each adult in each of the eight study families.

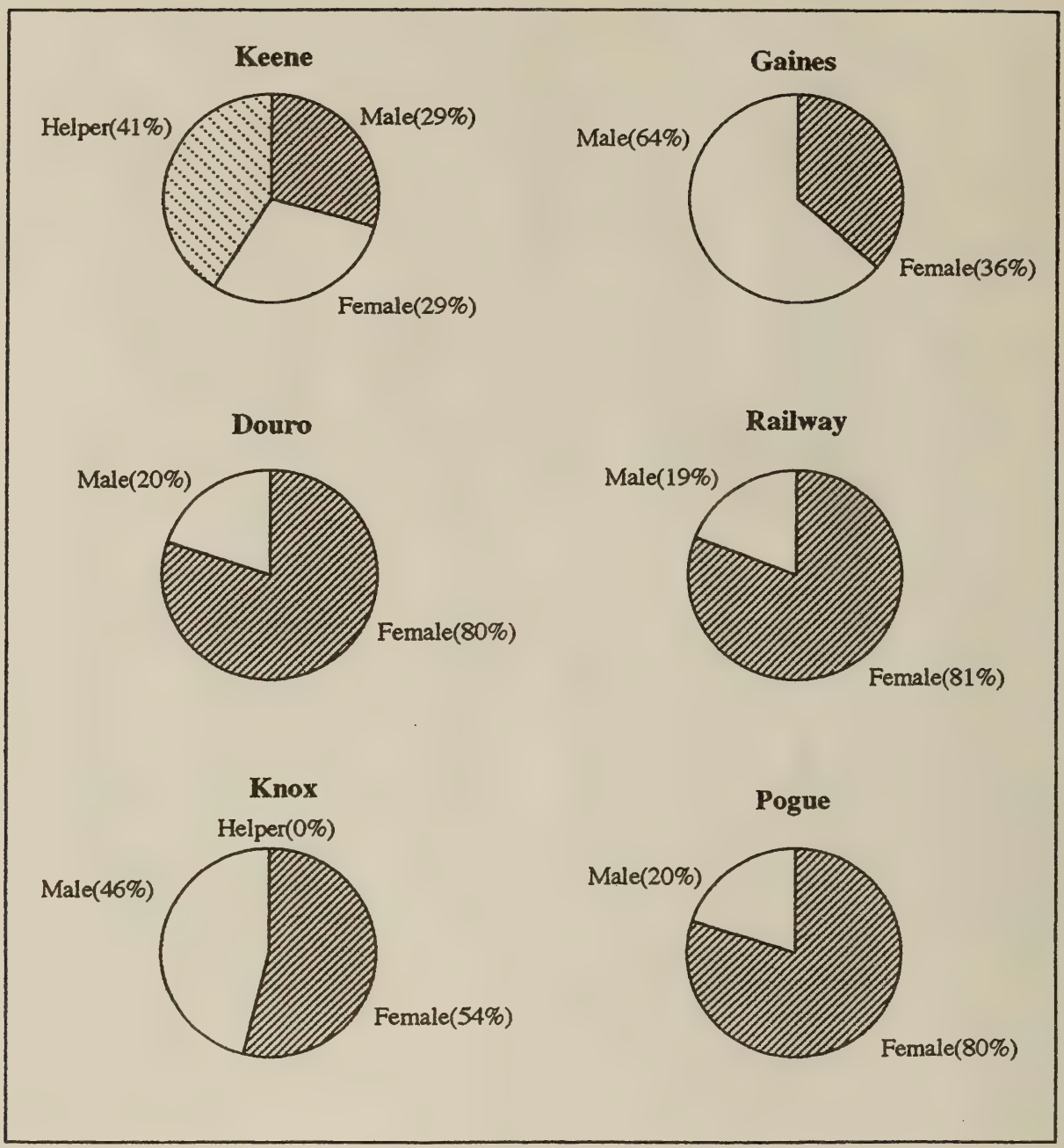

FIGURE 6. The relative contribution of each adult to feeding the kits in six families.

Adult distances from the kits

As shown in Figure 9, females spent most of their time at the den in contact with the kits (35 %), within 1 m (25%) and between 1 to 10 m (25 %) of the kits. Males, on the other hand, spent most of their time between 1 to 10 m (35 %), and between 10 to 20 m (19%) from the nearest kit. Males spent a higher proportion of their time than females at distances of 20 to 50 m (females 5 %, males 13 %) and 50 to 100 m (females 2 %, males 14 %). For the seven distance categories in Figure 9, a chi-square test of independence provides strong evidence that females remain closer to kits than do males (χ^2 = 763.238, df = 6, $P \leq 0.01$).

Patterns of parental care: presence of helpers

There were differences in parental behaviour between males and females, as well as between females of different families and males of different families (Vergara 1996 provides behavioural details for each individual). Furthermore, two families (Knox and Keene) had quite attentive fathers and an additional non-breeding adult (helper) that contributed to raising the young. The Keene helper was a female. Her gender was confirmed when the animal rolled over on its back or sat on its haunches. Also a squatting urination was observed. She visited the den site as often as the breeding female (0.17 visits/hour, Figure 2), showed the same behaviours than the adult female (excluding nursing) indicative of parental attentiveness, and contributed 41 % of the food items brought to the kits. The Knox third adult was only observed once, and

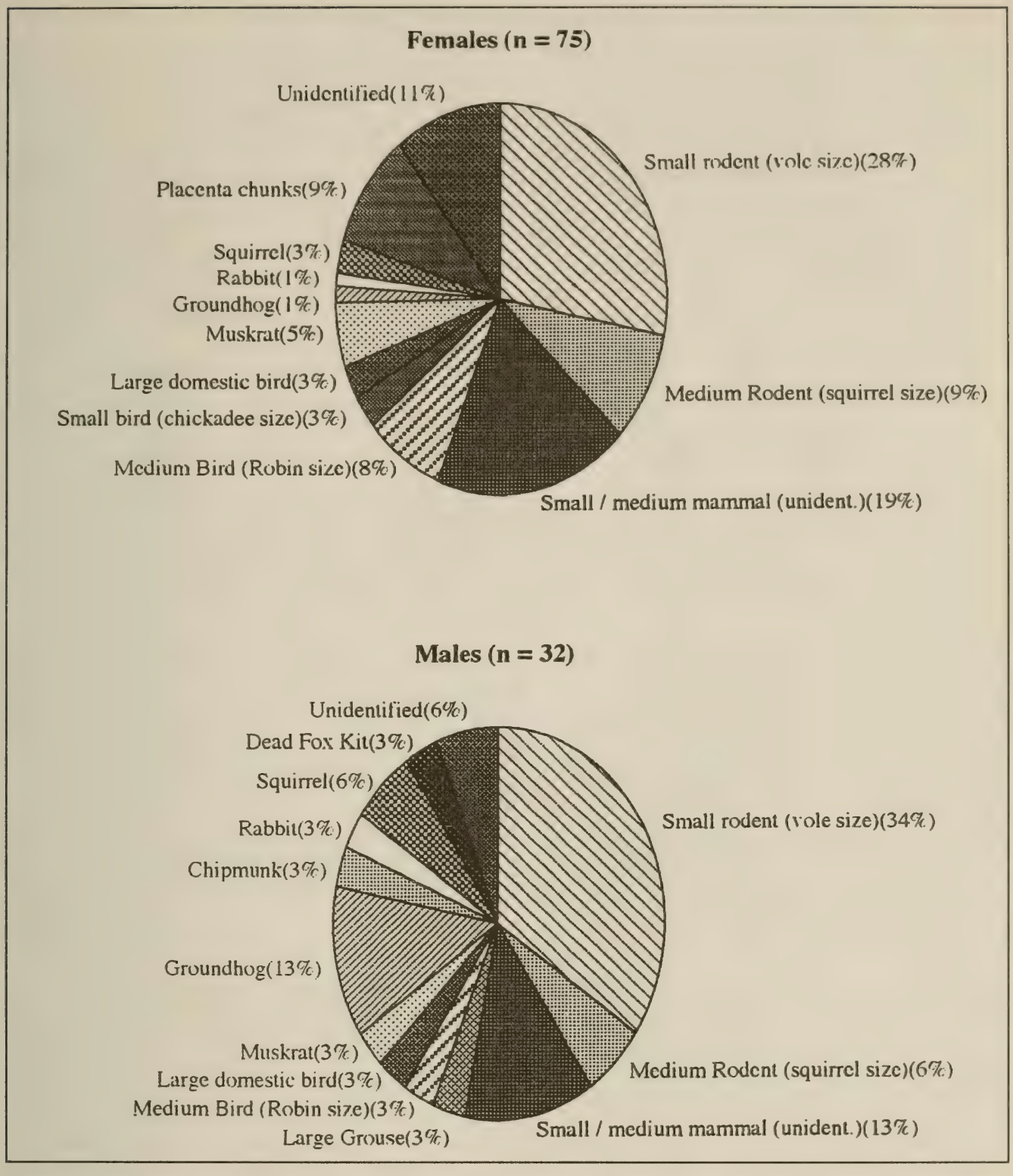

FIGURE 7. Food items observed being fed to kits by male and female Red Foxes in the eight study families (n = individual feedings).

its gender was not identified. Since it was greeted by the kits, and it groomed them and guarded them for a period of two hours in the absence of the breeding pair, I assumed it was indeed a helper (see Vergara 1996 for behavioral details on these helpers).

I cannot relate patterns of care (e.g., presence of helpers) to offspring survival since I did not observe the young until the age of independence.

Discussion

In general, this study shows that Red Fox males tend to contribute less direct care than females in raising the young. Apart from lactating, females were generally more interactive with the young, and stayed closer to the young than males. Females also visited the den more frequently and for longer periods of time than males. The number of trips/hour that one parent made to the den was independent of

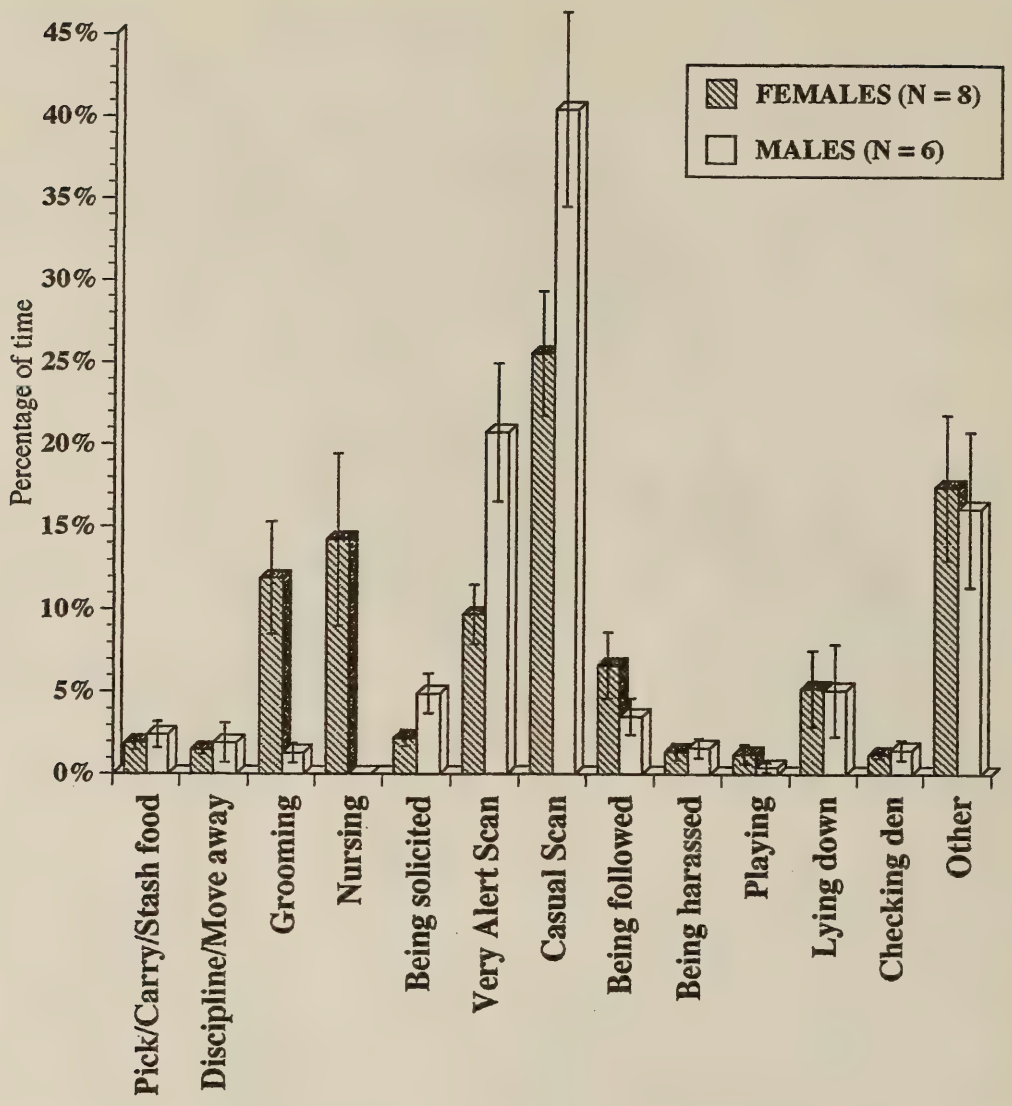

FIGURE 8. Average proportion of time that males and females spent in different behaviours, based on a total of 165 females visits and 58 male visits to the den. Vertical bars represent standard errors.

the number of trips/hour made by the other parent. Males did exhibit, to a lesser extent, the same direct parental care patterns as females. The difference was particularly marked when looking at behaviours that involved physical contact, such as grooming the kits. The combination of greater direct care and the energetic costs of gestation and lactation results in a greater total investment in direct care by female than by male Red Foxes.

To make conclusive statements about food provided to the kits, variations in the gross energetic content of the prey items should be taken into account. The size of the prey items brought to the den influences the energy intake of the young. Furthermore, some prey items may take more time and energy to hunt than others. The only real difference seems to be in the number of groundhogs brought to the den. However the numbers are relatively small (four groundhogs brought by males vs. one brought by a female), and the relative percentages of the other prey types do not seem to differ between males and females. Further studies should incorporate an analysis of the energetic aspects such as energy supply by different prey items, estimations of prey relative abundance and ease of capture.

There was some individual variation in parental behaviour among females (particularly in terms of grooming, nursing and contact rates with the young), and considerable variation among the males. There were three males that rarely visited the den (Douro, Railway, and Pogue), and provided less food items than females to the young. Three other males visited regularly (Keene, Gaines, and Knox) but showed different degrees of close interaction with the young. The Knox male barely interacted with the young and kept his distance from them, whereas the Gaines and Keene males were indeed quite affectionate to the young. In my study, only one father (Gaines) provided more food items to the kits than the mother (two thirds of the food items brought to the den).

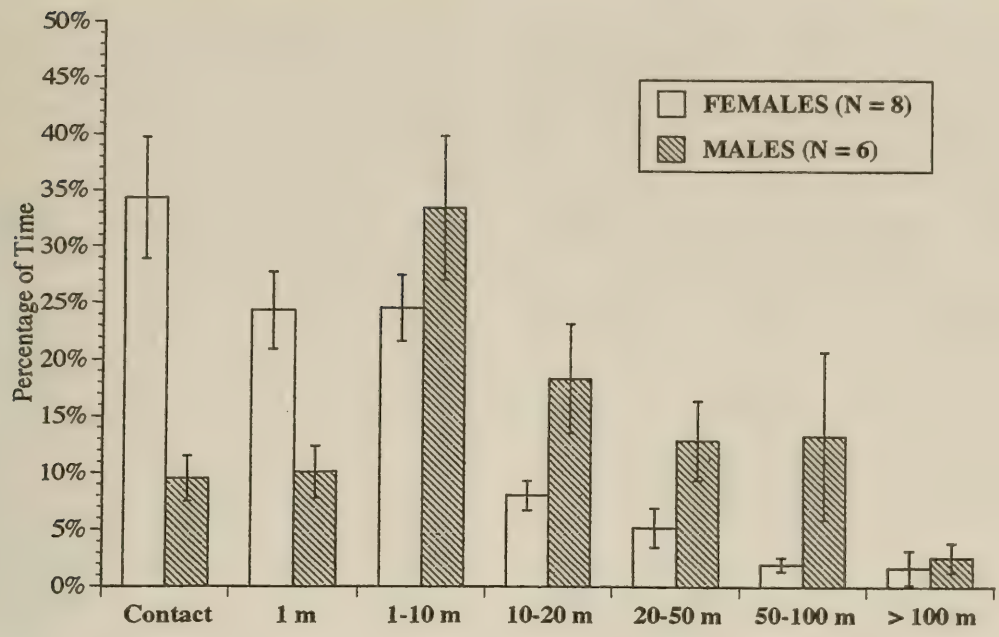

FIGURE 9. Average proportion of time that males and females spent at different distances from the nearest kit, based on 165 female visits and 58 male visits. Vertical bars represent standard errors.

However, dog foxes providing more food than vixens have also been reported in other studies. For instance, Macdonald (1979) found that the father of a captive Red Fox family group provided 41.1% of the food items to the kits, more than either the mother (21.2%), or the two helpers (17 % and 20 %). Finally, another aspect of the observed variability in parental care patterns is the presence of a helper in two of the families (Keene and Knox). In Ontario, evidence of several vixens within a family group, helping, and communal denning is sparse (Voigt and Macdonald 1984).

Intraspecific variation in paternal care is not unique to foxes. Male care in Coyotes (*Canis latrans*) was reported absent in some parts of their range (e.g., Minnesota, Berg and Chesness 1978) and present in others (e.g. Wyoming, Camenzind 1978). In fact, intraspecific variation in patterns of parental care and social organization in contrasting habitats may be as pronounced as interspecific differences (Macdonald 1980, and Moehlman 1989 for canids; Bekoff et al. 1984, for carnivores, citing examples of Coyotes, Wolves, Kalahari Lions, *Panthera leo*, Brown Hyenas, *Hyaena brunnea*, Striped Hyenas, *Hyaena vulgaris*, Golden Jackals, Raccoons, *Procyon lotor*, African Wild Dogs and Red Foxes; Moehlman 1998, for Feral Asses, *Equus africanus*; Roberts et al. 1998, for Prairie Voles, *Microtus ochrogaster*; Yamagiwa and Hill 1998, for Japanese Macaques, *Macaca fuscata*; Blumstein and Armitage 1999, for several species of Marmot, *Marmota spp.).*

Variability in the reproductive strategies of male foxes may be related to food, as it is well known that differences in food availability may be primarily responsible for intraspecific variation in carnivore social organization (Bekoff et al. 1984; Macdonald and Moehlman 1982). Examples in canids are prevalent (e.g. Coyotes: Bekoff and Wells 1982, Bowen 1981; Red Foxes: Englund 1980, Macdonald 1979, Zabel and Taggart 1989; Jackals: Ferguson et al. 1983, Moehlman 1983; African Wild Dogs: Frame et al. 1979). However, in this study I did not quantify and compare the resources available around the different den sites. Thus, any proposed relationship between the level of paternal care found in this study and the availability of food will remain a speculation, and invites further research.

The individual variability I observed could be simply explained as idiosyncratic differences. Such individual differences have been reported in other canid studies. For instance, Venkataraman (1998) noted significant differences across adult males in two Dhole, *Cuon alpinus*, packs in the frequency of pup-raising behaviours displayed at the den.

Indirect care

An important consideration when evaluating the extent of male care is the possibility that some individuals make most of their investment indirectly. My study indicates that dog foxes do invest less than vixens in direct parental effort. However, my results clearly show that males tend to spend significantly more time in sentinel behaviour than females. Vigilant behaviour is often considered a form of indirect male parental care. Indirect care may include activities which a male would perform regardless of the presence or absence of the young, but that may

increase the young's survivorship (Kleiman and Malcom 1981). The frequencies or proportions of these behaviours (such as very alert or casual scan in this study) may alter in response to the existence of young, even if direct care is not seen (Kleiman and Malcom 1981). It would be useful, but difficult, to compare vigilant behaviour in males and females when both are away from the young, in order to determine if the higher proportion of time spent scanning by males at the den sites is associated with the presence of young.

The importance of indirect forms of care should not be underestimated. In the present study, although males provided less direct care than females, they consistently scanned the area more than females. This behaviour may help to detect danger, such as Humans, Coyotes or strange foxes.

An additional indirect form of male care is shelter construction and maintenance (Kleiman and Malcom 1981). Few carnivore males are reported to take a major role in burrow construction (Kleiman and Malcom 1981). In my study, the Knox male contributed to the excavation of the woods den, where the family subsequently moved. This insures that the necessary resources (in this case, space) are available to the young.

This study supports the notion that for polygyny to occur, the female must be able to provide most of the offspring's needs. In Red Foxes, which exhibit a potentially monogamous, occasionally polygynous system, males contribute less than females to the direct care of the young, and their contribution is also qualitatively different.

The present study also corroborates the great flexibility in the behaviour of Red Foxes. Elucidating the ecological circumstances that promote this variation in both social groupings and patterns of parental care in southern Ontario should be an objective of further studies. Understanding the social structure, mating system, and patterns of parental care of any fox population requires an understanding of food dispersion and availability in such area. Thus, further studies of variation in paternal care should quantify and compare the resources available around the different den sites. Behavioural variation in male paternal care and the variation in female responses to different degrees of care by the male should be an important research priority.

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Biodiversité microfongique du *Fagus grandifolia* dans une forêt ancienne: bioindicateurs et structure mycosociologique

VLADIMIR VUJANOVIC[1,2] et JACQUES BRISSON[1]

[1]Institut de recherche en biologie végétale, Université de Montréal, 4101 est, rue Sherbrooke, Montréal, Québec H1X 2B2 Canada

[2]Département de Sciences biologiques, Université de Montréal, C.P. 6128, Succursale « Centre-ville », Montréal, Québec, H3C 3J7 Canada

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En Amérique du Nord, l'étude de la biodiversité des micromycètes dans les forêts anciennes représente un potentiel incontournable et largement inexploré. Le présent inventaire nous a permis de mettre en évidence la biodiversité microfongique, les bioindicateurs et la structure mycosociologique associée au hêtre à grandes feuilles (*Fagus grandifolia*) dans une forêt ancienne de l'est du Canada. La méthodologie utilisée s'appuie sur la stratégie proposée par le *All-Taxa Biodiversity Inventory of Fungi* (ATBIF). Plusieurs espèces s'avèrent des nouvelles mentions sur un hôte du genre *Fagus*. C'est le cas pour tous les membres de la sous-famille *Phialostromatinae* (*Deuteromycota, Coelomycetes*), soit quatre genres et cinq espèces, dont certaines pourraient être des espèces très rares ou menacées. Quatre associations, chacune étant associée à une partie spécifique de l'arbre, ont été déterminées. De plus, deux autres associations sont caractéristiques d'habitats particuliers dans la forêt. Notre étude supporte l'hypothèse selon laquelle les forets anciennes sont des écosystèmes en homéostasie qui constituent des réservoirs d'espèces microfongiques d'une grande diversité génétique. Outre la valeur intrinsèques de cette diversité exceptionnelle, les micromycètes ont également une valeur pratique potentielle, comme dans le contexte de la lutte biologique.

Mots clés: All Taxa Biodiversity Inventory (ATBI), biodiversité, micromycètes, bioindicateurs, coelomycetes, endophytes, hêtre, forêt ancienne, *Fagus grandifolia*, Québec.

Les micromycètes entretiennent des relations de parasitisme ou de mutualisme très intimes avec les plantes, insectes, animaux ou autres micro-organismes suite au processus de coévolution (Pirozynski et Hawksworth 1988). Ce groupe taxonomique est pourtant fort important, car on estime qu'il y a beaucoup plus d'espèces de micromycètes dans la nature que de plantes hôtes (Hawksworth 1991). Ces espèces microphongiques sont étroitement associées à des substrats particuliers, soit un hôte spécifique, à une partie d'un hôte (écorce, feuille, graines, etc.) ou encore à un stade de développement particulier (Lisiewska 1992). Ainsi, dans une biocénose fortement organisée comme dans une forêt âgée, le plus grand nombre de niches potentielles peut résulter en une plus grande biodiversité microfongique (Arnolds 1988). Les micromycètes sont davantage susceptibles de se comporter comme des indicateurs particuliers de l'âge de la forêt, mais aussi des changements environnementaux (Horn 1985; Miller 1989; Vujanovic 1994).

La forêt ancienne est reconnue par des arbres âgés, de grandes variétés de milieux, sa complexité et sa richesse biologique ainsi que ses communautés d'Organismes vivants (Carroll 1995; Stone et al. 1996). La communauté microfongique est une composante intégrale de ces milieux (McCutcheon et al. 1993) qui interagissent avec d'autres organismes selon la physionomie, la structure et de la couverture des arbres (Chapela 1989). Comme résultat, on détecte une variation de la distribution spatiale de micromycètes colonisateurs (Chapela et Bodddy 1988). Le paradigme de la colonisation des arbres vivants par des micromycètes est déterminé majoritairement par la position des niches écologiques; la lumière, la disponibilité de la chaleur et l'humidité (Boddy et Rayner 1983; Oshima et al.1997).

Le retard à combler dans la connaissance de la biodiversité fongique, l'augmentation de pathogènes virulents (CFS, 1997) et une diminution drastique de plusieurs de ces organismes utiles dû à l'influence de l'activité humaine (Roberts et Gilliam 1995) ont mené au développement d'une nouvelle stratégie scientifique, le *All-Taxa Biodiversity Inventory of Fungi* (ATBIF), une composante majeure du *All-Taxa Biodiversity Inventory* (ATBI) (Rossman 1994). Le ATBIF propose une méthodologie de réalisation d'inventaire qui tient compte de la variété des substrats (hôtes) et de la variation d'abondance des champignons dans l'espace et dans le temps. Cette stratégie s'avère particulièrement appropriée pour l'étude de la biodiversité des micromycètes dans un habitat, et sur une superficie limitée (Vujanovic et al. 1997).

La réserve écologique du Boisé-des-Muir est une forêt ancienne dominée par l'érable à sucre, le hêtre et la pruche. Avec ses arbres tricentenaires, elle serait une des dernières représentantes de la grande forêt décidue de l'Amérique du Nord, telle qu'elle existait à l'arrivée des premiers colons européens (Brisson et al.

1992). Conséquemment, elle est susceptible de révéler une biodiversité microfongique particulière incluant des espèces très rares et associées à des niches écologiques étroites. Notre étude préliminaire a permis la découverte de deux espèces de micromycètes nouvelles pour la science, le *Diarimella laurentidae* Vujanovic, St-Arnaud, Neumann & Fortin (Vujanovic et al. 1998) et le *Polynema muirii* Vujanovic, St-Arnaud, Neumann, Fortin & Brisson (Vujanovic et al. 1999a).

Il est généralement reconnu qu'une biodiversité spécifique est associée aux forêts en santé (Aplet et al.1993). Il y a donc une certaine urgence à mieux connaître la biodiversité du Boisé-des-Muir si on veut pleinement profiter des bénéfices de sa spécificité, car son intégrité écologique est menacée par l'introduction récente d'une maladie fongique exotique, la maladie corticale du hêtre (Vujanovic et Brisson 1999b). La maladie corticale menace de causer la disparition de certains micromycètes associés directement ou indirectement au hêtre, et l'augmentation d'espèces pathogènes ou de décomposeurs qui profiteront de l'affaiblissement du hêtre. À plus longue échéance, les changements climatiques et l'éventualité de plus en plus grande que des événements climatiques extrêmes, comme le récent verglas, viennent bouleverser l'équilibre de la forêt, favoriseront vraisemblablement une augmentation des maladies fongiques (Coakley 1995).

L'objectif principal de cette recherche est d'examiner la biodiversité microfongique, les bioindicateurs et la structure mycosociologique associée au parties aériennes du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) dans la réserve écologique du Boisé-des-Muir.

Méthodologie

La méthodologie utilisée s'appuie sur la stratégie développée par ATBIF (Rossman 1994). Étant donné que la diversité microfongique peut varier selon les situations édaphiques et phytosociologiques locales (Vujanovic 1995; Vujanovic et Vuckovic 1994), l'échantillonnage a été stratifié à l'aide des cartes de distribution des arbres de la réserve (Brisson et al. 1989) afin de couvrir tout le spectre des conditions locales.

Échantillonnage

L'échantillonnage a été effectué 2 fois, en automne 1996 et 1997. Un échantillonnage systématique a été réalisé en sélectionnant 45 arbres dont 15 dans chacune des catégories suivantes: étage supérieur, étage médian et sous-bois. Aussi, des parties vivantes et mortes ont été récoltées afin de couvrir à la fois les champignons pathogènes et décomposeurs. Au total, 1911 échantillons d'écorce ont été récoltés sur différentes parties de l'arbre: tronc (morceau d'écorce de 36 mm^2), branches (diamètre > 3 cm ; portions de branche échantillonnée de 10 à 20 cm de longueur), rameaux (diamètre = 0,5 à 3 cm; portions échantillonnées de 5 à 10 cm) et ramilles (diamètre < 0,5 cm portions échantillonnées de 1 à 5 cm).

Notons qu'étant donné le court mandat de cette étude, l'échantillonnage ne couvre qu'une partie de la biodiversité microfongique associée au hêtre car elle ne permet pas de couvrir les micromycètes apparents à d'autres moments de l'année (l'hiver, le printemps, l'été) ou sur d'autres parties de la plante (fruits, feuilles, graines). Les échantillons récoltés ont été placés dans des boîtes ou sacs stériles. Au moment du prélèvement, nous avons noté les traces de symptômes, la date de prélèvement et la localisation dans le boisé (Myren et al. 1994).

Isolation des micromycètes sur milieux de culture

Les échantillons ont été conservés dans les sacs stériles en plastique à l'obscurité dans un incubateur à 4°C, jusqu'à leur traitement. La procédure de l'isolation consiste : (i) stérilisation du surfaces des échantillons d'écorce et de rameau à l'aide de bain d'hypochlorite de sodium (0.5%); (ii) la préparation des milieux de culture (potato dextrose agar, czapeck agar, malt agar); (iii) l'inoculation d'une pièce d'écorce (8 mm^2) sur chacun des milieux, en trois répétitions; (iv) le repiquage et la purification des isolats et (v) la conservation des isolats sur milieux nutritifs selon la procédure développée par Dhingra and Sinclair (1987) et Booth (1971).

Identification

Les identifications de champignons ont été faites selon les caractères morphologiques et culturaux à l'aide des clés d'identification : *Microchampignons* selon Ellis et Ellis (1985) et Lanier et al. (1978); *Coelomycetes* selon Nag Raj (1993) et Sutton (1980); *Ascomycota* selon Hanlin (1990), Sivanesan (1984), Breintenbach et Kranzlin (1981), Dennis (1978), et Barr (1978); *Deuteromycota* selon Barnett et Hunter (1987); *Hyphomycètes* selon Ellis (1971). La nomenclature et la phylogénie adoptée est celle de Hawksworth et al. (1995). Étant donné la complexité souvent encore inexplorée associée au groupe des micromycètes, plusieurs des identifications réalisées se limiteront au stade du genre, et certains champignons demeureront même non identifiés.

Les spécimens microfongiques sur l'écorce portant des fructifications des micromycètes ont été déposés à l'Herbier Marie-Victorin (IRBV, MT: 10311-13260).

Statut des espèces trouvées

La biodiversité microfongique est si mal connue qu'il est souvent difficile de statuer sur la rareté des taxons identifiés. Les connaissances actuelles concernant le statut des espèces en Amérique du Nord en est à peine à l'étape de l'inventaire. La liste des micromycètes du Boisé-des-Muir a été comparée avec l'inventaire le plus récent des espèces trouvées au Québec (SPPQ 1996) au Canada (Ginns 1986), aux États-Unis (Farr et al. 1989). Enfin, nous avons quali-

fié la rareté des taxons à l'échelle du Boisé-des-Muir selon leur représentation dans les échantillons récoltés.

Résultats et Discussion

Biodiversité microfongique sur l'hôte du hêtre

Au total, 60 genres comprenant 76 espèces appartenant au *Ascomycota, Deuteromycota* (= Mitosporic Fungi) et au *Zygomycota* ont été isolés (Figure 1 et Tableau 1). Parmi ces espèces, 65 % des *Hyphomycetes*, 75% de *Coelomycetes* et 39% des *Ascomycotina* représentent les nouvelles mentions comme colonisateurs du hêtre au Canada (Figure 1). Pour le Québec, on parle de 84%, de 100%, et de 96%; et pour les États-Unis, de 58%, de 45% et suivi de 26%, respectivement. D'ailleurs, plusieurs espèces trouvées au Boisé-des-Muir n'avaient encore jamais été mentionnées sur un hôte du genre *Fagus*. C'est notamment le cas pour tous les membres de la sous-famille *Phialostromatinae* (classe *Coelomycetes*) trouvés au boisé (Figure 2), soit quatre genres i) *Diarimella*, ii) *Dinemasporium,* iii) *Polynema,* et iv) *Pseudolachnea*, comme le confirme la mise à jour de ce groupe de microchampignons réalisée par Nag Raj (1993).

Biodiversité microfongique selon la position dans l'arbre

Plusieurs espèces s'attaquent spécifiquement à une portion d'arbre, alors que d'autres s'avèrent ubiquistes (Tableau 1 et Figure 3).

I. Association : *Ustulineto-Nectrietum.* Au total 20 espèces caractérisent cette mycocénose. *Ustulina deusta* agent de la carie blanche et plusieurs *Nectria* spp. responsables de chancre nectrien colonisent la partie basse du tronc des vieux arbres, jusqu'à une hauteur de 3 m;

II. Association : *Hypoxylonetum.* Au total 9 espèces caractérisent cette mycocénose, dont celles du complexe de l'*Hypoxylon* spp. (chancre hypoxylonien). Elles dominent sur les premières branches de la couronne et sur la partie supérieure du tronc;

III. Association : *Quaternato-Diatrypetum.* La communauté microfongique associée aux rameaux (0.5-3 cm diam.) est représentée par les espèces pathogènes du complexe de *Dyatrype* spp. (dépérissement diatripéen). La biodiversité de cette mycocénose compte au total 28 espèces récoltées ;

IV. Association : *Valsetum.* Sur les ramilles (<0.5 cm. diam.), les espèces du complexe *Valsa* spp., anamorphe: *Cytospora* spp., (chancre cytosporéen ou dépérissement cytosporéen) dominent. Dix-sept espèces caractérisent cette mycocénose.

Parmi les genres ubiquistes, on retrouve *Verticillium*, *Trichoderma* et *Cladosporum.* Quelques-unes de ces espèces présentent un potentiel intéressant comme agent de lutte biologique, contre certaines maladies fongiques dont la maladie corticale du hêtre (Lonsdale 1982).

Dispersion horizontale des communautés microfongiques du Boisé-desMuir

Un traitement complémentaire a été fait dans l'optique d'enrichir l'analyse de la diversité par une information mycosociologique basée sur les bioindicateurs des habitats étudiées (Tableau 2).

$A_{1\text{-}6.}$ Association : *Ascodichaenetum.* L'apparition de l'espèce différentielle *Ascodichaena rugosa* et les quatre autres espèces (*Diatrypae, Botryosphaeria, Microdiplodia, Valsa*) est l'indicateur plus contribu-

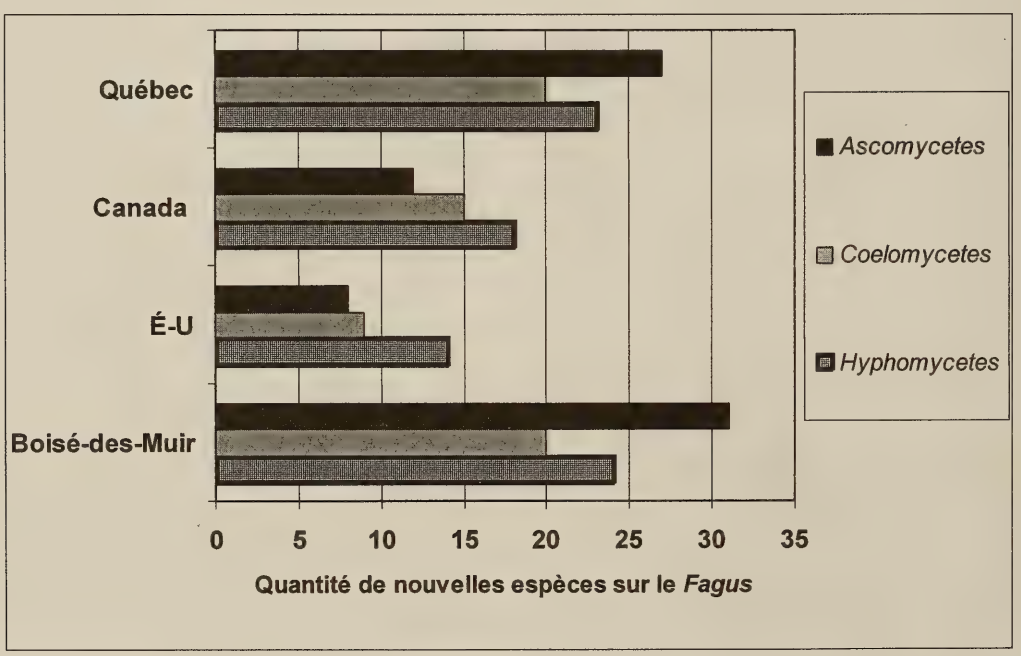
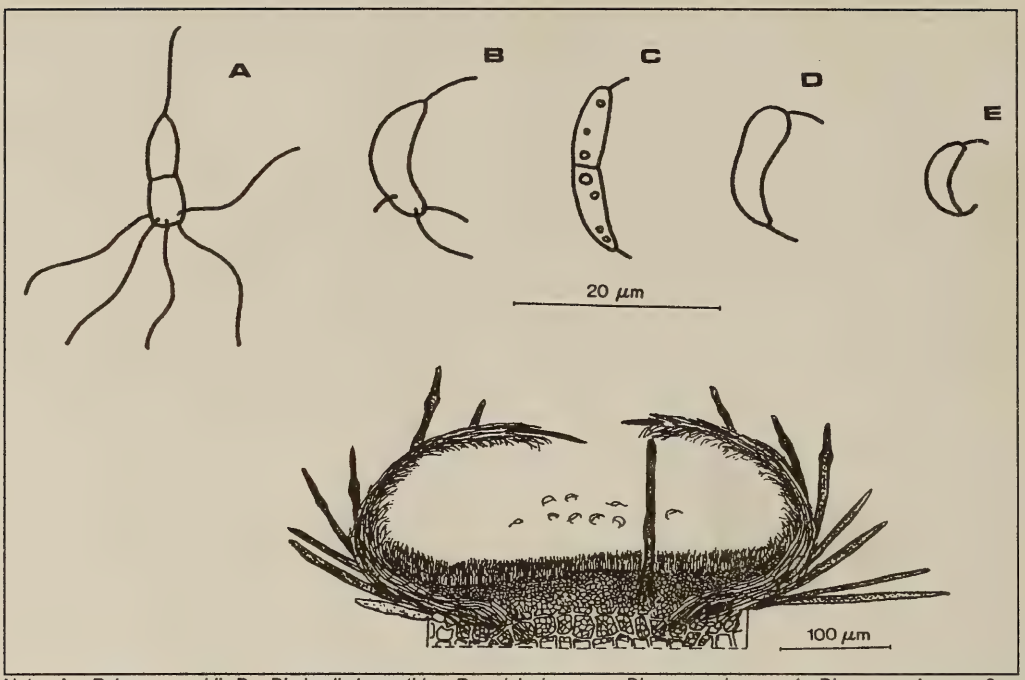


FIGURE 1. Niveau de connaissance de la biodiversité d'espèces des microchampignons du hêtre en Amérique du Nord

TABLEAU 1. Biodiversité microfongiques des phyla *Ascomycota, Deuteromycota* et *Zygomycota* sur l'écorce du hêtre (*Fagus grandifolia* Ehrh.) et des communautés microfongiques selon le vertical axis des arbres dans la forêt Boisé-des-Muir.

Brindille: Assotiation: *Valsetum* Vujanovic & Brisson	P	**Rameau:** Assotiation: *Quaternato-Diatrypetum* Vujanovic & Brisson	P	**Branche:** Assotiation: *Hypoxylonetum* Vujanovic & Brisson	P	**Tronc:** Assotiation: *Ustulineto-Nectrietum* Vujanovic & Brisson	P	**Ubiquistes**	P
Camarosporium sp.	H	*Asteromassaria macrospora* (Desm.) Höhnel	*A*	*Diatrype disciformis* (Hoffm.: Fr.) Fr.	A	*Ascodichaena rugosa* Butin	A	*Aureobasidium pululans* (de Bary) Arnaud	H
Coniothyrium fagi Techon	C	*Botryosphaeria* sp.	A	*Hypoxylon cohaerens* (Pers.: Fr.) Fr.	A	*Asterosporium asterospermum* (Pers.:Fr.) Hugh	C	*Alternaria alternata* (Fr.:Fr.) Keissl.	H
Cytospora sp.	C	*Cytospora* sp.	C	*Hypoxylon fragiforme* (Pers.: Fr.) Fr.	A	*Coniothyrium fagi* Techon	C	*Acremonium* sp.	H
Diarimella laurentidae Vujan et al.	C	*Diarimella laurentidae* Vujanovic et al.	C	*Hypoxylon rubiginosum* (Pers.: Fr.) Fr.	A	*Durella* sp.	A	*Ampelomyces* sp.	H
Dinemasporium sp.-1	C	*Dinemasporium* sp.-1	C	*Hypoxylon mammatum* (Wahl.) J.H. Mill.	A	*Hypoxylon fragiforme* (Pers.:Fr.) Fr.	A	*Botritys cinerea* Pers.:Fr	H
Dinemasporium sp.-2	C	*Diplodia* sp.	C	*Microdiplodia* sp.	C	*Hypoxylon mammatum* (Wahl.) J.H. Mill.	A	*Cladosporium cladosporioides* (Fr.) De Vries	H
Eutypella sp.	A	*Dasyscyphus* sp.	A	*Nectria* sp.	A	*Hypoxylon rubiginosum* (Pers.: Fr.) Fr.	A	*Cladosporium herbarum* (Pers.: Fr.) Link	H
Fusicoccum sp.	C	*Diatrype disciformis* (Hoffm: Fr.) Fr.	A	*Neohendersonia kickxii* (West.) Sutt. & Pol.	A	*Hypoxylon cohaerens* (Pers.:Fr.) Fr.	A	*Cylindrocarpon* sp.	H
Libertella faginea Desm.	C	*Diatrype stigma* (Hoffm: Fr.) Fr.	A	*Quaternaria quaternata* (Pers.) Chroter	A	*Karstenula* sp.	A	*Cylindrocarpon destructans* (Zinss.) Scholten	H
Phoma sp.	C	*Diatrype* sp.	A			*Lasiosphaeria* sp.	A	*Cylindrocladium* sp.	H
Phomopsis oblonga (Desm.) Trav.	C	*Durella* sp.	A			*Massarina* sp.	A	*Endophragmiella* sp.	H
Phyllosticta sp.	C	*Eutypella* sp.	A			*Microthyrium* sp.	A	*Epicoccum nigrum* Link	H
Polynema muirii Vujan. et al.	C	*Fusicoccum* sp.	C			*Leptographium* sp	H	*Epicoccum purpurascens* Echrenb.	H
Pseudolachnea sp.	C	*Hypoxylon cohaerens* (Pers.: Fr.) Fr.	A			*Microdiplodia* sp.	C	*Fusarium oxysporum* Schl.:Fr.	H
Uncinula sp.	A	*Hypoxylon fragiforme* (Pers.: Fr.) Fr.	A			*Nectria coccinea* (Pers.:Fr.) Fr.	A	*Fusarium* sp.	H
Valsa ambiens (Pers.:Fr.) Fr.	A	*Hypoxylon mammatum* (Wahl.) J.H. Mill.	A			*Nectria* sp.	A	*Gliocladium* sp.	H
Valsa sp.	A	*Libertella faginea* Desm.	C			*Nectria galligena* Bres.	A	*Hendersonia* sp.	H
		Mollisia sp.	A			*Trematosphaeria* sp	A	*Leptographium* sp.	H
		Nectria cinnabarina (Tode: Fr.) Fr.	A			*Ustulina deusta* (Fr.) Petrak	A	*Mucor racemosus* Fresen.	Z
		Neohendersonia kickxii (West.) Sutt. & Pol.	C			*Xylaria polymorpha* (Pers.:Fr.) Grev.	A	*Nectria episphaeria* (Tode:Fr.) Fr.	A
		Phoma sp.	C					*Penicillium* sp.	H
		Phomopsis oblonga (Desm.) Trav.	C					*Pecilomyces farinosus* (Holm.) Brown &Sm.	H
		Pseudolachea sp.	C					*Pleospora* sp.	A
		Quaternaria quaternata (Pers.) Chroter	A					*Rhynocladiella* sp.	H
		Scolicosporium sp.	C					*Rhizopus* sp.	Z
		Trematosphaeria sp.	A					*Trichoderma harizanum* Rifai	H
		Valsa ambiens (Pers.: Fr.) Fr.	A					*Trichoderma viridae* Pers.:Fr.	H
		Valsa sp.	A					*Verticillium lecanii* (Zimm.) Viég.	H

Note : P — Phylum; A — Ascomycota, C: Deuteromycota — *Coelomycetes* ; H: Deuteromycota – *Hyphomycetes*; Z: Zygomycota



Note : A – *Polynema muirii* ; B – *Diarimella laurantidae*; *Pseudolachnea* sp. ; *Dinemasporium* sp.–1 ; *Dinemasporium* sp.–2

FIGURE 2. Nouvelle subfamille *Phialostromatinae* (Coelomycètes) pour l'hote du genre *Fagus* d'origine des isolats du Boisé-des-Muir

tive du coté positif, concernant d'humidité modéré. Six localités typiques du mesohabitat mésique sont déterminées. *Ascodichaena rugosa* est l'espèce épiphitique sur l'écorce vivante du hêtre, particulièrement bien installé sur la partie basal du tronc. Il se comporte comme l'antagoniste de la maladie corticale du hêtre — *Nectria coccinea*. L'abondance et la fréquence de fructifications sont en fonction de l'âge de l'hôte ainsi qu'en fonction du changement de la structure d'écorce (Butin, 1977).

$B_{1\text{-}5.}$ Association : *Ustulinetum*. L'apparition de l'espèce différentielle *Ustulina deusta* et les quatre autres espèces (*Asterosporium, Asteromassaria, Massarina, Xylaria*) indique, du coté négatif, caracteristiques de milieu plus humide. Cinq localités typiques de mésohabitat hydrique sont identifiées. La pathogène *U. deusta* cause un chancre basal sur le tronc d'arbres submatures. De plus, l'association est indicative d'un sol mal drainé et la présence d'eau stagnante d'un microhabitat forestier (Sinclair 1993). L'apparition de fructifications est premier signe de la mortalité d'un arbre (Lisiewska 1992).

Conservation de la diversité génétique des micromycètes aux forêts anciennes

Les résultats de notre recherche, pourtant préliminaire, sur les micromycètes à la réserve écologique du Boisé-des-Muir nous ont permis de mettre en évidence la biodiversité remarquable de ce groupe dans les forêts anciennes. Une grande quantité d'espèces répertoriées comme endophytes sont à leur première mention du genre *Fagus* (Figure 1.) tant au Canada (59%), au Québec (93%), qu'en États-Unis (43%) et même à l'échelle mondiale. Deux d'autre, elles ont d'ailleurs été récemment décrites (Vujanovic et al. 1998; Vujanovic et al. 1999a). Ce premier constat est d'ailleurs incomplet car plusieurs espèces récoltées sont restées non identifiées.

Bien qu'une partie importante des découvertes réalisées dans le cadre de notre étude peut être attribuée au manque de connaissances générales sur la répartition et l'abondance des organismes fongiques, il n'y a toutefois pas de doute que la réserve écologique Boisé-des-Muir possède une diversité microfongique exceptionnelle et unique. Cette réalité est confirmée, également, par le nombre de communautés fongiques trouvées lors de cette étude et par la complexité de leur dispersion verticale sur le hêtre (Figure 2). Certaines autres espèces différentielles distribuées horizontalement sont considérées comme bioindicateurs d'habitats mésique ou hydrique du hêtre. À l'aide de celles-ci, on reconnaît deux sub-associations différentes de forêt du Boisé-des-Muir (Tableau 2). Les conditions environnementales d'un habitat mésique (subassociation *Acereto-Fagetum grandifoliae*) peuvent permettre à l'initiation et à l'établissement de communautés microfongiques beaucoup plus rapidement qu'avec un habitat hydrique (subassociation Acereto-Fraxinetum nigrae), ainsi que leur succession (Auclair and Goff 1971). Mais au cours du temps, une des associations microfongiques « hydriques » (association *Ustulinetum*) deviendra considérablement plus riche en nombre d'espèces par rapport à une association « mésique » (ass. *Ascodihaenetum*) (Burton et al. 1992).

Notre inventaire préliminaire supporte l'hypothèse selon laquelle les forêts anciennes sont des écosys-

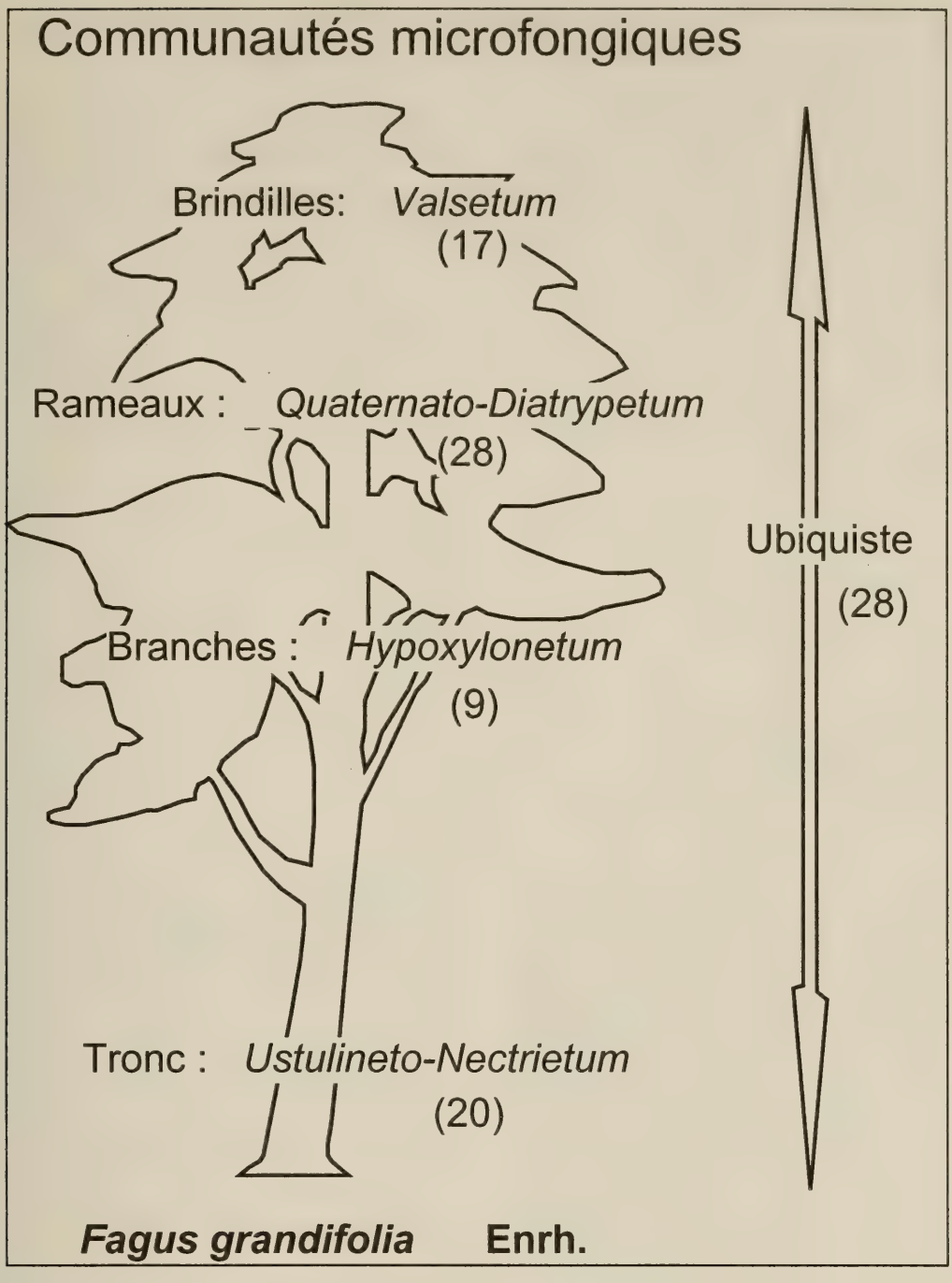


FIGURE 3. La distribution spatiale des mycocénoses caractéristiques avec le nombre d'espèces associé au parties aériennes du Hêtre.

tèmes en homéostasie (Roberts and Gillam 1995) qui constituent des réservoirs d'espèces microfongiques d'une grande diversité génétique (Stone et al 1996). Toutefois, pour être en mesure de pleinement apprécier le caractère distinctif de la biodiversité des forêts anciennes, il faudrait établir des comparaisons précises avec des données quantitatives récoltées dans les forêts aménagées (Hansen et al. 1991), sous des conditions abiotiques similaires, données qui sont pour le moment inexistantes.

Les stress environnementaux tel que celui du verglas de janvier 1998 peuvent modifier la composition microfongique et favoriser les groupes pathogènes (Coakley 1993). La réduction en biomasse de la couronne peut augmenter significativement le risque d'une progression de la maladie corticale du hêtre et l'infection par des pathogènes secondaires (Woodcock et al. 1995) ou encore la disparition d'espèces microfongiques rares ou vulnérables (Christensen and Emborg 1996) .

Outre la valeur intrinsèque de leur diversité exceptionnelle, les micromycètes ont également une valeur pratique potentielle, comme dans le contexte de la lutte biologique. D'ailleurs, l'exploitation commerciale de biopesticides à base de champignons est déjà bien établie dans le monde entier (ARS 1997). L'utili-

TABLEAU 2. Dispersion horizontale des communautés microfongiques comme bioindicateur des mesohabitats caractéristiques du Boisé-des-Muir.

Communauté microfongique	Espèces différentielles des micromycètes		Mesohabitat		
Type		**Sub-associations de forêt**	**Condition hydrique**	**Condition édaphique**	**Condition topographique**
Ascodichaenetum Vujanovic & Brisson **[A_1-A_6]**	*Ascodichaena rugosa*, *Diatrypae* sp., *Botriosphaeria* sp., *Microdiplodia* sp., *Valsa* sp.	***Acereto-Fagetum grandifoliae*** Espèces differentieles: *Acer saccharum*-50% *Fagus grandifolia* -15% *Tilia americana*-10% *Tsuga canadensis*-5% etc.	Mésique	Brunisol distrique ortique Drainage modéré	Petit sommet Pente 1–5%
Ustulinetum Vujanovic & Brisson **[B_1-B_6]**	*Ustulina deusta*, *Asterosporium asterospermum*, *Asteromassaria marospora*, *Massaria* sp., *Xylaria polymorpha*	***Acereto-Fraxinetum nigrae*** Espèces differenciels: *Fraxinus nigra*-25% *Ulmus americana* — ? *Acer saccharum*-20% *Tilia americana*-20% *Fagus grandifolia* -5% etc.	Hydrique	Brunisol eutriphique gleyifié Drainage mal drainé	Dépression

sation de micromycètes dans le cadre d'une lutte contre la maladie corticale du hêtre semble aussi présenter un potentiel intéressant (Houston et al. 1979). Bernier et al. (1996) ont constaté qu'une diversité plus grande de micromycètes offre une plus grande chance de trouver des antagonistes. Aussi, il a été démontré que certaines espèces des genres *Cladosporium* sp., *Nectria* sp., *Verticillium* sp. et *Paecilomyces* sp. peuvent, en culture *in vitro*, parasiter la cochenille du hêtre (Lonsdale 1982). Dans le cadre de notre inventaire, nous avons remarqué que la maladie était absente si la communauté d'*Ascodichaenetum* était présente. Plusieurs autres espèces, notamment les ubiquistes, pourraient avoir des propriétés antagonistes face à la maladie corticale du hêtre (Lonsdale 1982). Enfin, nous avons isolé et identifié plusieurs espèces de champignons hyperparasites ou antagonistes de la cochenille ou du champignon responsable de la maladie corticale. Ces espèces peuvent constituer une base solide pour le développement d'une lutte biologique efficace. Le potentiel d'utilisation de micromycètes dans la lutte contre la maladie corticale ne constitue qu'un exemple des bénéfices pratiques que ces organismes représentent.

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Influence de paramètres climatiques sur les patrons d'activité saisonniers et journaliers du lièvre d'Amérique, *Lepus americanus*, en semi-liberté

JÉRÔME THÉAU[1] et JEAN FERRON[2]

Département de biologie et des sciences de la santé, Université du Québec à Rimouski , 300 allée des Ursulines, Rimouski, Québec G5L 3A1 Canada

[1]Adresse actuelle: Centre d'Études Nordiques, Université Laval, Sainte-Foy, Québec G1K 7P4 Canada (courriel : j.theau@courrier.cen.ulaval.ca)

[2]Auteur de correspondance: courriel: jean_ferron@uqar.uquebec.ca

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L'activité du lièvre d'Amérique (*Lepus americanus*) a été observée au cours d'un cycle annuel entier afin de déterminer les patrons d'activité à l'échelle saisonnière et journalière et d'étudier l'effet de paramètres climatiques sur ceux-ci. L'activité de six individus a été enregistrée par une caméra vidéo dans un enclos de 1350 m^2, situé dans un boisé et muni d'une station météorologique informatisée. La température, l'humidité relative, la vitesse du vent et la pression barométrique ont été enregistrées toutes les 5 minutes durant la période d'échantillonnage. Dix séquences de 24 heures consécutives, réparties sur l'année, ont permis d'étudier le cycle d'activité journalier selon les saisons de reproduction et d'inactivité sexuelle. 72 heures d'observations mensuelles ont également permis d'analyser les patrons d'activité journaliers et d'évaluer l'impact des facteurs climatiques sur ceux-ci. Les résultats montrent que les lièvres sont principalement actifs à l'aurore, au crépuscule et durant la nuit. Ils adaptent cependant leurs niveaux d'activité entre les saisons afin de bénéficier des conditions favorables de température dans la journée. A plus court terme, les températures basses ou en diminution ainsi qu'une humidité relative haute ou en augmentation favorisent l'activité. Une augmentation de pression barométrique favorise également l'activité. Les risques de prédation et les besoins énergétiques expliqueraient ces différents patrons d'activité.

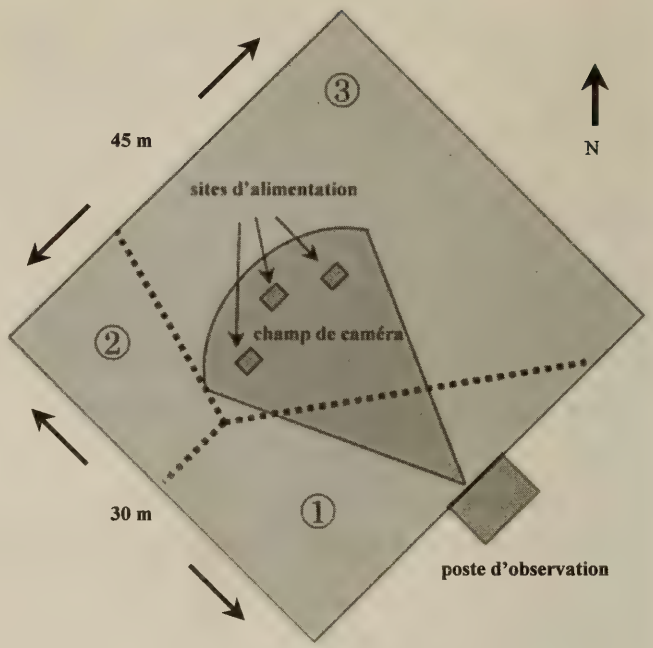
Snowshoe Hare *(Lepus americanus)* activity was observed during a one-year period to analyze the effect of environmental factors on activity at a seasonal and daily scale. The activity of six animals was recorded by video camera in a 1350 m^2 outdoor enclosure located in a wood stand and equipped with a computerized weather station. Temperature, relative humidity, wind speed and barometric pressure were recorded every 5 minutes during the study period. Ten 24-hour sequences were recorded to compare activity during the breeding and the non-breeding seasons. Each month, 72 hours of observation were used to study activity pattern within a day, and to analyze the impact of climatic factors on activity. Results indicate that, year round, hares are mainly active at dawn and dusk, and during the night. They, however, adjust their level of activity seasonally, in order to take advantage of favorable temperature conditions during the day. On a short-term basis, they increase their activity at low or diminishing temperatures, and at high or increasing relative humidity. An increase in barometric pressure also stimulates hare activity. Predation risks and energetic requirements could explain the different patterns of activity.

Mots clés : Lièvre d'Amérique, *Lepus americanus*, patrons d'activité, facteurs climatiques, cycle annuel, semi-liberté, Québec.

L'activité, chez les animaux comme chez l'homme, regroupe les comportements impliquant une dépense énergétique (Colgan 1978). Le déplacement, la quête de nourriture, les interactions sociales ainsi que le toilettage font partie de cette catégorie. Il n'existe cependant pas de mesure directe et universelle de l'activité. Les auteurs utilisent des signes indirects pour la quantifier. Les traces laissées sur divers substrats peuvent notamment servir à cette fin (Vickery et Bider 1981). Le temps passé à la quête de nourriture (Gilbert et Boutin 1991), la présence d'individus dans le champ d'observation (Villafuerte et al. 1993), le temps passé à différents comportements (Lemnell et Lindlöf 1981; Homolka 1986), le nombre de déplacements (Matuszewski 1981) ou le nombre de captures pendant la période d'activité (Seabloom et al. 1994) constituent les principaux indicateurs utilisés. La télémétrie sert également à quantifier l'activité grâce à des colliers qui émettent des signaux spécifiques au mouvement ou à l'immobilité de l'animal (Drew et Bissonette 1996). Les facteurs environnementaux tels que la température, l'humidité relative, le vent ou les précipitations, entre autres, ont un impact important sur les patrons d'activité des lagomorphes comme l'ont montré Villafuerte et al. (1993) chez le lapin de garenne (*Oryctolagus cuniculus*), Homolka (1986) chez le lièvre d'Europe (*Lepus europaeus*), Lemnell et Lindlöf (1981) chez le lièvre variable européen (*Lepus timidus*), Kline (1965) chez le lapin à queue blanche (*Sylvilagus floridanus*) et Gray (1993) chez le lièvre arctique (*Lepus arcticus*). Le risque de prédation constitue aussi un facteur notable influençant les patrons d'activité (Curio 1976; Pépin et Cargnelutti 1994; Moreno et al. 1996). Les facteurs environnementaux

jouent cependant un rôle indirect dans ce cas puisque la luminosité peut intervenir dans la détection des prédateurs par les lièvres. Il est généralement admis que les lagomorphes sont moins actifs lorsque la luminosité est élevée, qu'il s'agisse de la lumière du soleil ou de la lune, afin de limiter leur exposition aux prédateurs (Keith 1964; Gilbert et Boutin 1991; Villafuerte et al. 1993). Enfin, pour certains auteurs, les facteurs environnementaux ne feraient que renforcer des patrons d'activité déjà conditionnés par des mécanismes endogènes chez un grand nombre d'espèces, y compris des lagomorphes (Aschoff 1966).

Chez le lièvre d'Amérique, Bider (1961), Keith (1964), Mech et al. (1966) et Alain (1986) mentionnent le caractère crépusculaire et nocturne de cette espèce. Selon Gilbert et Boutin (1991), la luminosité de la lune, lorsqu'elle est forte, semble cependant réduire l'activité des lièvres à découvert. Pour Bider (1961), la vitesse du vent constitue l'effet le plus restrictif sur l'activité, en hiver. Cependant, ces résultats sont issus, pour la plupart, d'observations ponctuelles effectuées sur une seule saison ou de manière qualitative. Il existe donc un réel besoin d'étudier le cycle d'activité du lièvre d'Amérique, tant sur une base annuelle que circadienne et d'évaluer l'impact des facteurs environnementaux sur ces différents patrons. L'objectif de la présente étude est donc de décrire les patrons circadiens et saisonniers d'activité du lièvre d'Amérique et d'évaluer l'impact des paramètres climatiques sur ceux-ci.



① Zone sans couvert arborescent
② Zone de chablis
③ Zone boisée

FIGURE 1. Schéma de l'enclos (non à l'échelle) incluant les divers types de couverts végétaux, les sites d'alimentation et le champ de la caméra durant la période d'étude.

Matériel et Méthodes

Echantillonnage

Enclos

Cette recherche a été effectuée à St-Anaclet, Québec (48°31'N, 68°24'W), de mai 1997 à avril 1998, dans un enclos de 30 m × 45 m, situé dans un boisé (Figure 1). La végétation était constituée d'une zone boisée principalement en thuyas (*Thuja occidentalis*) et en épinettes noires (*Picea mariana*) de hauteurs variant entre 2 et 5 mètres environ, d'une zone de chablis accidentée et riche en abris ainsi que d'une zone ouverte herbacée. Les prédateurs terrestres et aériens avaient un accès limité à l'enclos grâce à la clôture métallique (mailles de 5 cm, sauf le premier 60 cm où le maillage était de 1 cm), à un fil électrifié placé à sa base et à un réseau de fils d'aciers d'environ 2 mm de diamètre tendus à 2.5 m du sol formant des mailles d'environ 30 cm, ce qui n'a pas empêché les prédateurs de roder autour de l'enclos. Un seul animal a été victime de prédation au cours de l'étude.

Facteurs climatiques

Une station météorologique informatisée (Weather Monitor II™, Davis Instrument, Hayward, California, USA), située dans l'enclos, permettait de recueillir la température, l'humidité relative, la vitesse du vent ainsi que la pression barométrique toutes les cinq minutes durant la période de l'étude. D'autres facteurs ont été calculés à partir de ces données météorologiques et utilisés dans les analyses. « écart d'humidité relative », « écart de température » et « écart de pression barométrique » représentent l écart du facteur climatique concerné entre le début et la fin de chaque sous-période de 3 heures (voir la section: séquences d'enregistrement ci-dessous).

Individus

Six individus adultes capturés dans la région d'étude ont été observés (4 mâles et 2 femelles). En hiver 1997, une femelle est morte. Un mâle, préalablement acclimaté dans un enclos de rétention, a aussitôt été introduit afin de maintenir une densité constante. Afin de limiter l'effet de la compétition pour la nourriture, les individus ont été nourris *ad libitum* durant toute la période de l'étude avec de la moulée commerciale. Ils se sont également alimentés avec la végétation naturelle de l'enclos. Afin de faciliter les observations, la végétation a été tondue à plusieurs reprises dans le champ d'observation. Afin de maintenir une densité constante, les levrauts étaient retirés de l'enclos dès leur sevrage, au bout de quatre semaines environ.

Activité

L'activité a été notée sans distinguer les individus, en disposant deux fils verticalement sur l'écran de

télévision, de manière à diviser le champ d'observation en trois parties égales. Chaque franchissement d'un de ces fils par un individu était compté comme une unité d'activité dont le total était noté toutes les 5 minutes de façon synchronisée avec les données météorologiques à l'aide d'un gestionnaire de bases de données (Access® de Microsoft®). Cet indice d'activité a été choisi puisqu'il tient compte de l'activité liée aux comportements d'alimentation et sociaux.

Séquences d'enregistrement

Les observations d'activité ont été effectuées à partir d'enregistrements à l'aide d'une caméra vidéo (Video camera recorder CCD V220 Sony™) et d'un magnétoscope (Time lapse vidéo cassette recorder VT-L2000 AR Hitachi™). Le système vidéo localisé dans le poste d'observation (Figure 1) a permis de programmer des séquences à différentes périodes de la journée. Le champ de vision, constant tout au long de l'étude, était situé au centre de l'enclos, au niveau de la zone d'alimentation. Pour les séquences nocturnes, un projecteur à lampe au sodium contrôlé par une cellule photoélectrique permettait d'éclairer la zone filmée.

Dix séquences de 24 h consécutives chacune, réparties également sur toute l'année, ont été enregistrées afin d'observer l'activité du groupe durant un cycle journalier. Parallèlement, six journées additionnelles ont été échantillonnées chaque mois, constituées chacune de quatre périodes de trois heures: lever du soleil (1h30 avant et après), milieu de journée, coucher du soleil (1h30 avant et après) et milieu de la nuit.

Analyse des données

Cycle d'activité sur 24 heures

Les données d'activité recueillies par séquence de cinq minutes ont été additionnées par heure afin d'avoir un taux horaire d'activité. Une moyenne de ces taux a été effectuée pour chaque heure de la journée. L'année a été séparée selon la période de reproduction (avril à septembre) et de non reproduction (octobre à mars) (adapté de Ferron 1993), comprenant chacune 5 séquences enregistrées de 24 heures. Les moyennes horaires de température ont également été calculées pour chaque période et superposées aux données d'activité. La répartition de l'activité selon la période de la journée a été testée à l'aide des données d'activité par sous-période de trois heures (voir ci-dessous) afin de valider les résultats observés pour les cycles d'activité de 24 heures.

Répartition de l'activité selon la période de la journée

Les données d'activité recueillies par séquence de cinq minutes ont été transformées en taux horaires pour chaque sous-période de trois heures. Les analyses ont été effectuées sur les moyennes périodiques de ces taux d'activité horaires.

Une Anova à un facteur, suivie de tests de comparaisons multiples en utilisant la méthode de Bonferroni, a été utilisée pour tester les différences entre les taux d'activité moyens des quatre sous-périodes de la journée (lever du soleil, milieu du jour, coucher du soleil et milieu de la nuit). L'approche de Conover (1980) qui consiste à comparer une Anova non paramétrique sur les rangs à une Anova paramétrique lorsque les résidus ne correspondent pas aux conditions d'application a été utilisée pour ces tests. Les résultats de l'Anova paramétrique étaient utilisés lorsque les deux tests donnaient les mêmes résultats.

Influence des facteurs climatiques

L'influence des différents paramètres climatiques sur l'activité a été analysée en utilisant des Anova de Conover suivies de tests de comparaisons multiples selon la méthode de Bonferroni. Ces tests ont été effectués sur les moyennes des taux horaires d'activité compilées selon des classes définies pour chacun des facteurs climatiques. Ces classes ont été choisies afin de regrouper les données climatiques brutes sur une échelle plus synthétique.

Des analyses en composantes principales (ACP) ont également été utilisées afin de visualiser la variabilité saisonnière des relations entre les facteurs climatiques et l'activité. Nous avons appliqué les ACP à une matrice de corrélation des taux horaires d'activité et des moyennes des différents facteurs climatiques. Ces éléments ont été calculés pour chaque sous-période de trois heures. La méthode de rotation de la matrice selon la variance maximale a été utilisée afin de calculer le pourcentage de variance expliquée pour les deux principaux axes.

Le logiciel SYSTAT® (version 7.0.1 pour Windows®) a été utilisé pour effectuer les analyses statistiques (Wilkinson 1996). Les conditions d'application pour les tests paramétriques ont été vérifiées.

Résultats

Cycle d'activité sur 24 heures

L'activité journalière des individus présente des tendances comparables à l'année. L'activité est faible durant la journée et présente des pics au lever et au coucher du soleil (Figure 2). La nuit, l'activité reste modérée.

Certaines différences apparaissent également entre la période de reproduction et de non reproduction. L'activité au lever du soleil est plus concentrée lors de la période de reproduction alors qu'en période de non reproduction, cette tendance est observée au coucher du soleil. Parallèlement à ces observations, on note que pour les deux périodes de l'année, la température horaire suit un patron identique. Le moment le plus froid de la journée est situé au lever du soleil puis la température aug-

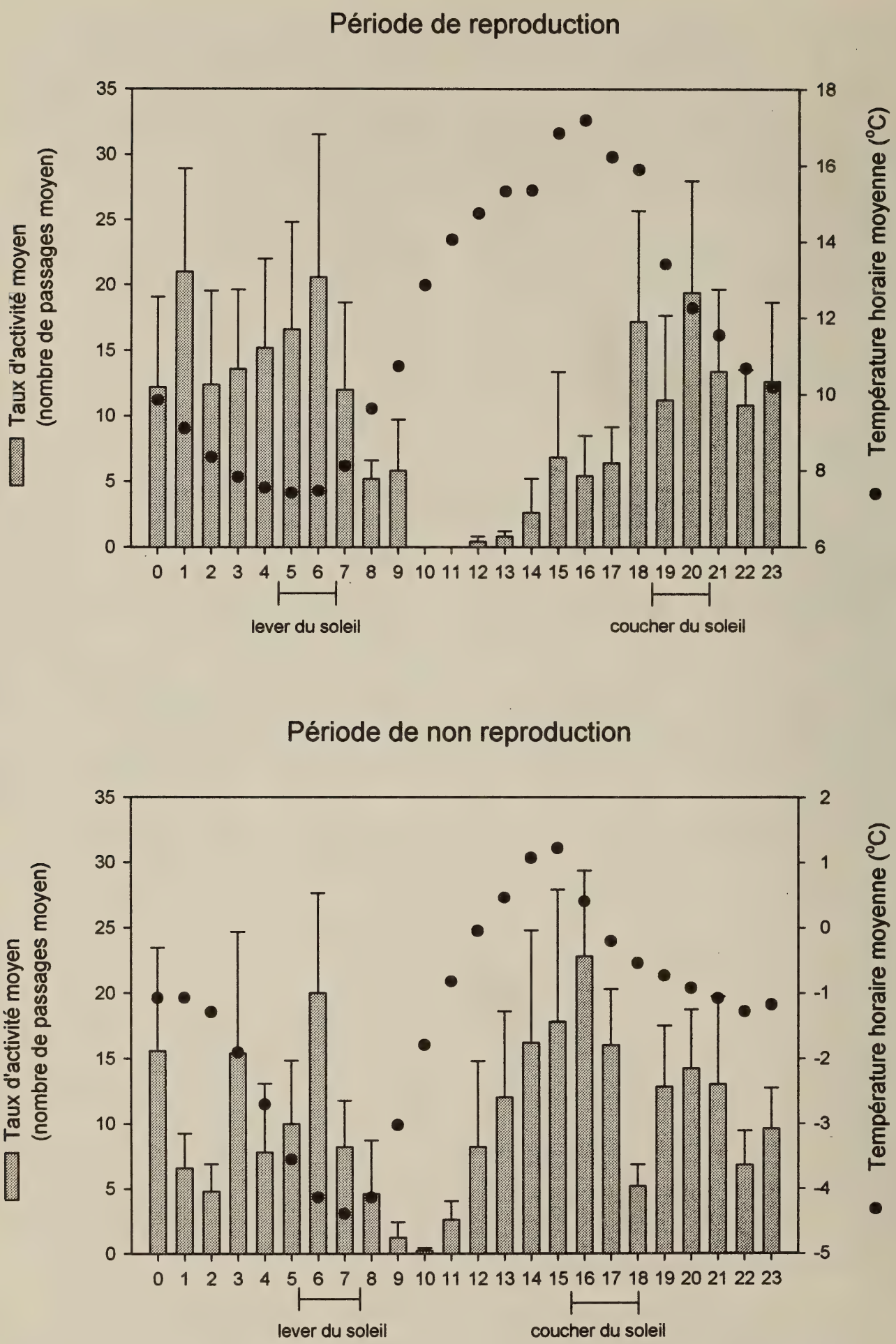


FIGURE 2. Cycle d'activité journalier du lièvre d'Amérique et température moyens selon la saison de reproduction.

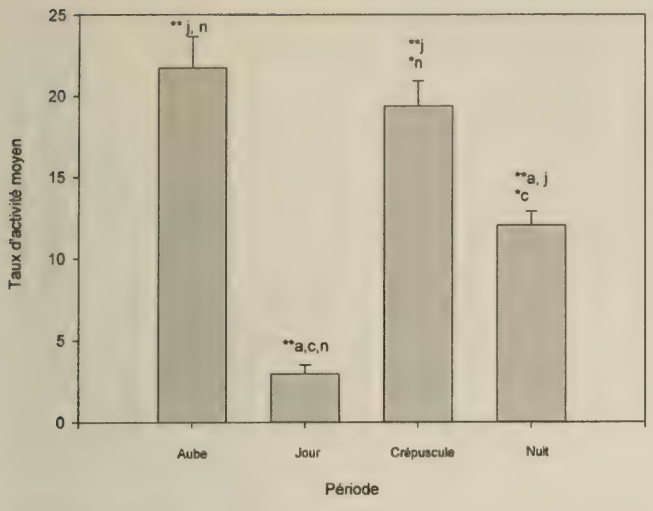


FIGURE 3. Taux d'activité moyen du lièvre d'Amérique selon les périodes de la journée: l'aube (a), le jour (j), le crépuscule (c) et la nuit (n). Résultats d'une Anova de Conover à un facteur suivie d'un test de comparaisons multiples selon la méthode de Bonferroni (**$p < 0.01$ et *$p < 0.05$).

mente pour atteindre son maximum juste avant le coucher du soleil.

Niveaux d'activité selon la période de la journée

Les résultats présentés à la figure 3 confirment les observations effectuées pour le cycle journalier d'activité. Les taux d'activité moyens à l'aube, au crépuscule et au milieu de la nuit sont plus élevés qu'au milieu de la journée. La nuit, le niveau d'activité modéré observé sur 24 heures se traduit par une moyenne significativement inférieure aux périodes de lever et de coucher du soleil, qui elles, ne présentent pas de différences entre elles. Les données d'activité basées sur les séquences de 3 heures dans la journée semblent donc représentatives de l'activité sur 24 heures puisqu'on observe les mêmes tendances dans les deux échantillonnages. La prise de données par séquence nous a permis d'effectuer un plus grand nombre d'observations et d'avoir une idée plus précise de l'influence des paramètres climatiques.

Influence des paramètres climatiques

Comme on peut le voir à la figure 4, les lièvres présentent deux niveaux d'activité selon la température. À des températures inférieures à 5°C, les taux d'activité sont significativement plus élevés qu'à des températures plus chaudes. Cette tendance est également observée par rapport aux variations de température dans chaque sous-période de 3 heures. Les individus sont, en effet, plus actifs lorsque la température est en diminution plutôt qu'en augmentation. Cependant, cette tendance est moins nette pour les valeurs extrêmes.

En ce qui concerne l'humidité relative, les individus semblent plus sensibles aux variations durant la sous-période (écart d'humidité relative), qu'à la valeur absolue de ce paramètre. En effet, on observe une activité plus élevée à partir de la classe [-3 0[, c'est-à-dire lorsque l'humidité demeure relativement stable ou qu'elle augmente. Lorsqu'il y a baisse d'humidité relative, les individus semblent moins actifs. Cette tendance est moins nette lorsqu'on met en relation l'activité avec les valeurs ponctuelles d'humidité relative. Seules les valeurs extrêmes présentent des différences significatives, les individus étant nettement moins actifs à très faible humidité et plus actifs à très haute humidité.

L'écart de pression barométrique à l'intérieur d'une sous-période de trois heures semble également avoir un effet sur le niveau d'activité. Lorsque la pression est en diminution, les taux d'activité sont nettement plus faibles que lorsqu'elle augmente. Deux classes correspondant à des diminutions de pression présentent des différences significatives avec 4 classes correspondant à des augmentations de pression.

Nos résultats ne mettent pas en évidence de différences significatives entre les taux d'activité et la vitesse du vent. On observe cependant une tendance négative entre les deux.

À l'échelle saisonnière, la figure 5 présente les relations entre les paramètres climatiques et l'activité. Au printemps et en été, l'axe 1 est créé par l'opposition entre la température (T) et l'humidité (H), l'activité étant fortement corrélée négativement avec le premier et positivement avec le second. La différence de pression barométrique (DP) et la vitesse du vent (V) caractérisent également cet axe. L'axe 2, créé par l'opposition entre l'écart de température (DT) et d'humidité relative (DH) présente moins d'influence sur l'activité pendant ces deux saisons.

En automne et en hiver, l'axe 1 est créé par l'opposition entre l'écart de température (DT) et d'humidité relative (DH) qui présentent, respectivement, de fortes corrélations négative et positive avec l'activité. La différence de pression barométrique s'ajoute à la formation de l'axe 1 en automne. Durant, cette dernière saison, la température (T) et l'humidité (H) sont corrélées à l'activité avec une importance plus grande pour la température. Par contre, c'est en hiver que la situation est la plus différente. En effet, l'activité semble être en relation plus grande avec les différences de température (DT) et d'humidité relative (DH) qu'avec les autres facteurs.

Discussion

Patrons journaliers d'activité

Nos résultats montrent que le lièvre d'Amérique est principalement actif au crépuscule et à l'aube et que sa principale période d'activité est concentrée durant la nuit, entre ces deux moments de la journée et cela pendant toute l'année. Ce patron d'activité a déjà été décrit chez cette espèce (Mech et al. 1966; Keith 1974), ainsi que chez d'autres lagomorphes comme le lapin de garenne (Villafuerte et al. 1993),

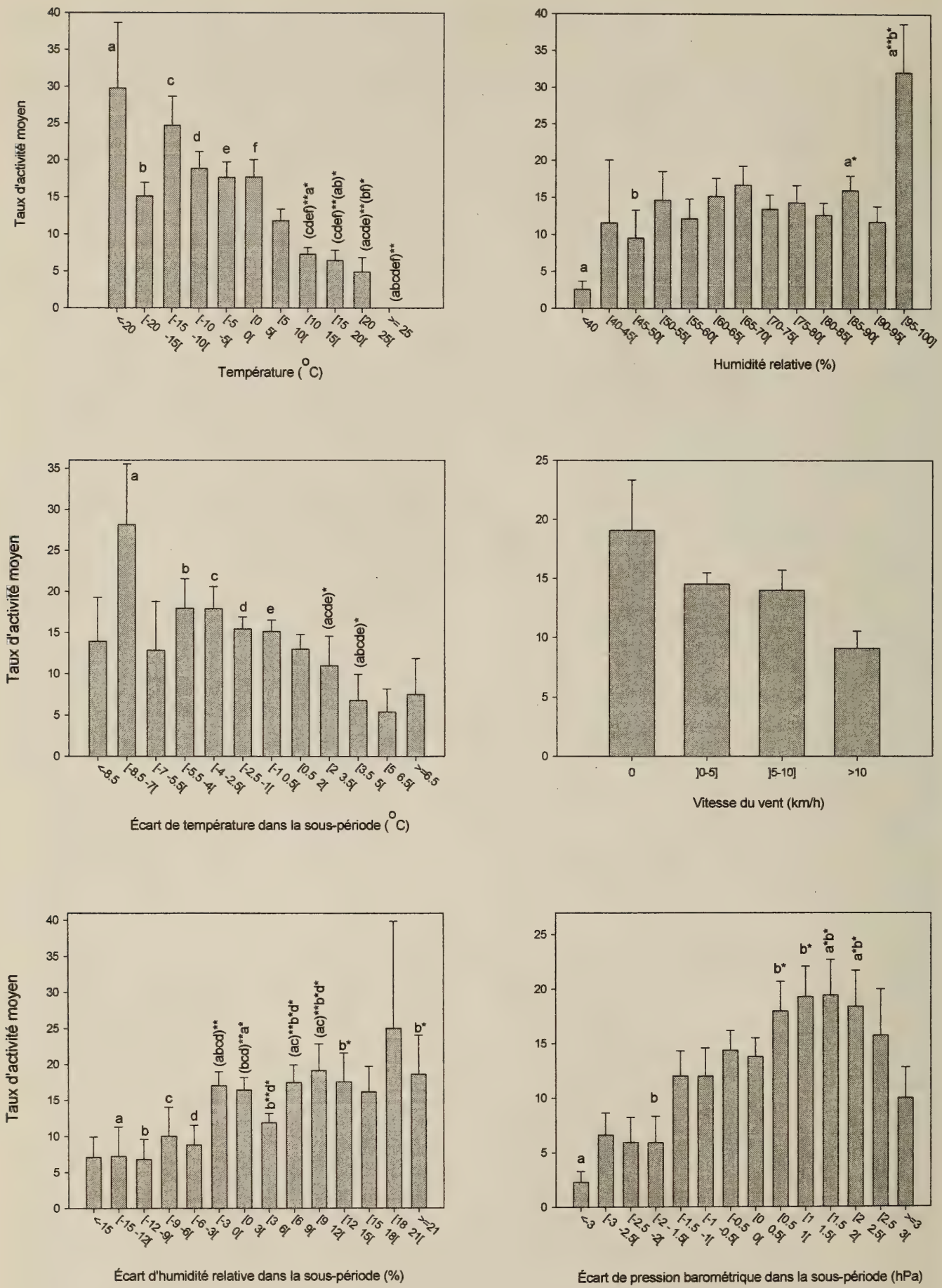

Taux d'activité moyen
Température (°C)
Humidité relative (%)
Écart de température dans la sous-période (°C)
Vitesse du vent (km/h)
Écart d'humidité relative dans la sous-période (%)
Écart de pression barométrique dans la sous-période (hPa)

FIGURE 4. Taux d'activité du lièvre d'Amérique en fonction de différents facteurs climatiques. Résultats des Anova à un facteur avec l'approche de Conover et des tests de contraste selon la méthode de Bonferroni (**$p < 0.01$ et *$p < 0.05$).

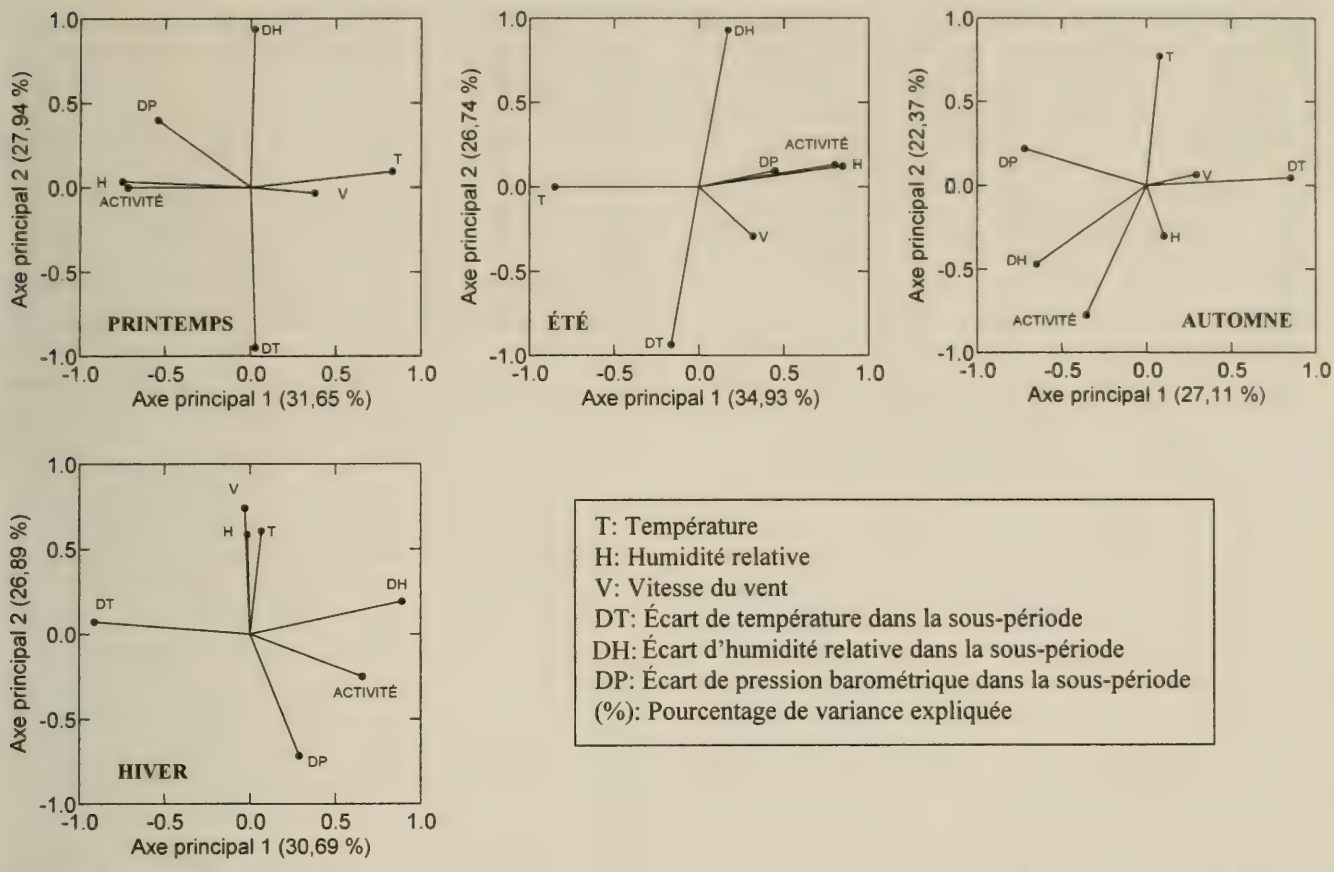


FIGURE 5. Analyses en composantes principales saisonnières des facteurs climatiques et des taux d'activité du lièvre d'Amérique.

le lièvre d'Europe (Homolka 1986; Pépin et Cargnelutti 1994) et le lièvre variable européen (Lemnell et Lindlöf 1981). Nos résultats apportent cependant certaines nuances par rapport aux travaux effectués par Keith (1964) qui ont décrit l'activité du lièvre d'Amérique selon une courbe symétrique sur 24 heures et dont le pic se situe à 23 heures. Ces résultats provenaient de données prises pendant un été seulement. Nos résultats permettent également d'apporter des nuances aux travaux effectués par Foresman et Pearson (1999) qui ont décrit l'activité du lièvre comme étant exclusivement nocturne durant l'hiver. Nos observations, effectuées sur une année entière, indiquent que l'activité du lièvre est effectivement concentrée entre le coucher et le lever du soleil mais qu'elle est davantage manifeste à l'aube et au crépuscule, et cela durant toute l'année. Le patron journalier d'activité d'un grand nombre d'espèces de proies est influencé par celui de leurs prédateurs (Curio 1976). Ces espèces synchronisent leur rythme d'activité inversement à celui de leurs prédateurs. Chez le lièvre d'Amérique, un niveau d'activité accru au coucher et au lever du soleil permettrait de limiter les contacts avec les prédateurs diurnes et nocturnes qui cessent ou débutent leur période d'activité à ces moments de la journée. Le très faible niveau d'activité observé pendant le jour serait également lié aux risques de prédation. Pendant cette période, les individus sont en effet plus vulnérables puisqu'ils sont exposés aux prédateurs chassant à vue. Les facteurs expliquant l'observation de patrons d'activité à deux pics ne font cependant pas l'unanimité. Aschoff (1966) mentionne que même si des stimuli environnementaux tels que l'aube ou le crépuscule peuvent accentuer ce type de patron, leur origine demeure cependant endogène. Cet auteur se base sur des expérimentations effectuées sur de nombreuses espèces animales qui montrent que même en l'absence de stimuli externes (ex : conditions de luminosité ou de température constantes), le patron circadien d'activité à deux pics reste présent jusqu'à une période d'un an chez une espèce de pinson (*Fringilla coelebs*). L'observation de ce type de patron chez un grand nombre d'espèces est donc probablement lié à la combinaison de facteurs externes et endogènes. Même si ce patron à deux pics reste constant tout au long de l'année chez le lièvre, nos résultats montrent que selon les saisons, certaines modifications du niveau d'activité se produisent et semblent, en partie, reliées à la température.

En effet, en superposant la température moyenne horaire aux taux d'activité, il apparaît qu'en période de non reproduction, les individus favorisent les heures les plus chaudes de la journée. Lors de cette période, qui correspond aux mois froids de l'année,

les températures les plus hautes sont observées au coucher du soleil et correspondent aux taux d'activité les plus élevés de la journée. En réduisant leur niveau d'activité lors de la partie la plus froide de la journée, les individus limiteraient leurs pertes d'énergie. Inversement, lors de la période de reproduction, qui correspond au printemps et à l'été, les individus semblent éviter les périodes les plus chaudes de la journée puisqu'ils sont principalement actifs autour du lever du soleil. Ils limiteraient ainsi leurs pertes d'eau par évaporation qui peuvent être importantes lorsque les températures sont élevées (Hart et al. 1965). Villafuerte et al. (1993) ont également observé ces mêmes changements de niveaux d'activité entre les saisons à l'intérieur de la journée chez le lapin de garenne. Le harcèlement par les insectes, au printemps et en été, pourrait également expliquer une activité accrue lors des périodes les plus froides de la journée puisque le dérangement est plus important lorsqu'il fait chaud. Cet effet a été documenté chez le caribou (*Rangifer tarandus*). Mörschel et Klein (1997) ont en effet montré que la présence d'insectes à des températures élevées affecte les caribous en causant une augmentation du temps passé debout et une diminution de l'alimentation.

Impact des facteurs climatiques

Le lièvre d'Amérique adapte ses niveaux d'activité entre les saisons et il bénéficie d'un pelage variable au cours de l'année qui lui assure une isolation thermique relativement efficace (Hart et al. 1965). Cependant, il emmagasine très peu de réserves énergétiques et doit se nourrir régulièrement sur de courtes périodes. Malgré ces adaptations, il doit donc s'exposer aux conditions climatiques rigoureuses et adopter des stratégies d'activité à plus court terme lui permettant de maintenir sa balance énergétique.

Ces stratégies se reflètent dans nos résultats par une activité plus élevée lorsque les températures sont basses ou en diminution et lorsque l'humidité relative est élevée ou en augmentation. Il est difficile de dissocier l'effet de la température et de l'humidité car ces deux facteurs sont fortement corrélés, toute l'année. Cependant, au printemps et en été, les lièvres semblent plus sensibles aux niveaux d'humidité et de température, alors que durant l'automne et l'hiver, ce sont les variations de ces facteurs à l'intérieur des périodes qui occupent un grand rôle dans les patrons d'activité observés. Sur toute l'année, lors de conditions froides ou de refroidissement, nos résultats d'activité refléteraient une augmentation de l'alimentation puisqu'une étude connexe (Théau et Ferron 2000) a montré une relation inverse entre la fréquence d'alimentation et l'écart et le niveau de température. Dans cette étude, le comportement d'alimentation était très fortement relié au déplacement, qui constitue notre indicateur d'activité. Les besoins énergétiques accrus lors de périodes froides ou de refroidissements rapides peuvent expliquer ces patrons d'activité. De façon générale, les tendances d'activité observées par rapport aux autres facteurs climatiques supportent également les résultats obtenus par Théau et Ferron (2000), en ce qui concerne les comportements d'alimentation et de déplacement. Les lièvres semblent notamment réagir aux chutes de pression, qui accompagnent le mauvais temps, en diminuant leur niveau d'activité et en l'augmentant lorsque la pression barométrique est en augmentation. Il est cependant difficile d'isoler et d'interpréter l'impact de la pression car elle est corrélée avec de nombreux autres facteurs (Marten 1973) et même si son effet a été mis en évidence chez d'autres espèces (Ables 1969; Marten 1973; Beltràn et Delibes 1994), les mécanismes physiologiques reliés à sa perception et à son mode d'action sur le comportement ne sont pas connus. Seule la vitesse du vent ne présente pas d'influence significative sur l'activité, bien que la tendance observée montre un impact négatif. Comme la vitesse du vent réduit la fréquence des comportements de toilettage, de déplacement et d'alimentation du lièvre (Théau et Ferron 2000), ceci suggère également que ce facteur climatique influence négativement l'activité en général. Les variations saisonnières de l'influence de ce facteur pourraient cependant expliquer l'absence de relation significative sur une base annuelle. En effet, contrairement à la situation rencontrée au printemps, en automne et en hiver, l'activité semble favorisée par temps venteux, en été. La diminution du harcèlement causé par les insectes pourrait expliquer ce patron d'activité.

Nos résultats confirment donc que les lièvres sont principalement actifs à l'aurore et au crépuscule et qu'ils sont nocturnes. De plus, ils adaptent leurs niveaux d'activité au cours de l'année en réagissant différemment aux facteurs climatiques entre les saisons, afin notamment de bénéficier des conditions de température journalière favorables. À l'échelle journalière, ils réagissent également à très court terme aux changements de conditions climatiques en modifiant leurs niveaux d'activité afin de limiter leurs pertes énergétiques.

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Fall Food Habits and Reproductive Condition of Fishers, *Martes pennanti*, in Vermont

KYLE R. VAN WHY and WILLIAM M. GIULIANO[1]

Wildlife Biology Program, Department of Biological and Environmental Sciences, California University of Pennsylvania, California, Pennsylvania 15419, USA

[1]Present address: Louis Calder Center – Biological Field Station, Fordham University, 53 Whippoorwill Road., P.O. Box K, Armonk, New York 10504, USA

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We examined 197 Fishers harvested in Vermont during December 1996, to determine (1) differences in diet among Fishers of different age, sex, mass, fat reserves, and female reproductive condition, and (2) differences in female reproductive condition among Fishers of different age, mass, and fat reserves. Fishers had a diverse diet, consuming 31 different items. Most of the diet was mammalian (72%), with avian prey (15%) and fruit (10%) of secondary importance. Diets were similar ($P > 0.10$; Morisita's index > 0.80) among Fishers of different ages (juvenile, yearling, adult), sex, body mass (< 2, 2–3.5, > 3.5 kg), and fat reserves. Reproductive condition (i.e., number of corpora lutea) of females increased with age ($P = 0.001$), but did not depend on level of fat reserves ($P = 0.297$), body mass ($P = 0.719$), or diet ($P = 0.665$).

Key Words: Fisher, *Martes pennanti*, age, diet, fat reserves, reproductive condition, sex, Vermont.

Fishers (*Martes pennanti*) are secretive, primarily carnivorous mammals long prized for their pelage (Douglas and Strickland 1987). As a predator, Fishers can play an important role in community dynamics (Douglas and Strickland 1987; Nudds 1987; Powell and Zielinski 1994), and may be indicators of community health in mature forest systems (Powell and Zielinski 1994). Historically, Fisher populations have fluctuated in response to a variety of factors, including changing furbearer harvest regulations, fur prices, and land-use practices such as timber harvesting (Allen 1987; Novak 1987; Obbard et al. 1987; Powell and Zielinski 1994). As fur harvest regulations become more restrictive and fur prices decline, changes in land-use may be most important to Fisher population dynamics. These changes in habitat may negatively impact Fisher reproduction and survival, by altering cover and prey availability (Douglas and Strickland 1987).

Little is known about Fishers in Vermont, where farm abandonment, timber harvest, and urbanization are changing the landscape. Thus, increased knowledge of Fisher ecology is important to its conservation. Our purpose was to better understand Fisher food habits and reproduction in Vermont to improve the scientific basis for conservation of the species. Specifically, we determined differences in diet among Fishers of different age, sex, mass, level of fat reserves, and female reproductive condition, and examined differences in female reproductive condition among Fishers of different age, mass, and physical condition in December.

Methods

We obtained 197 skinned Fisher carcasses collected from trappers by Vermont Department of Fish and Wildlife personnel during the 1996 trapping season (6–21 December). Animals were harvested throughout the state. Each carcass was weighed, sexed, and assigned an ocular visceral-fat rank, as an index to the level of fat reserves (1 = no fat to 4 = large fat deposits; Giuliano et al. 1989). We determined age by examining cementum annuli of a lower canine tooth (Johnston et al. 1987). To index reproductive condition of females, we removed the right ovary, preserved it in formalin (10%) for 24 hours, and then transferred it to ETOH (10%) until processing. Ten cross-sections of each ovary were mounted on slides to determine the number of corpora lutea, which we used as an index to reproductive condition (Douglas and Strickland 1987).

We removed stomachs and intestines from each carcass and rinsed contents through a 0.5 mm sieve. Prey remains such as bones, hair, seeds, etc. were identified macroscopically by comparison to reference collections. We identified trace amounts of hair to species by microscopic identification of guard hair pigmentation and comparison to reference specimens (Stains 1958).

We compared body mass between sexes and among ages (juvenile [<1 yr], yearling [1 yr], adult [≥2 yrs]) by analysis of variance (ANOVA) and, when necessary, a Fisher's LSD test. Differences in number of corpora lutea were compared among ages using an ANOVA followed by a Fisher's LSD test. We compared body mass between females with corpora lutea to those without using ANOVA. Differences in the level of fat reserves were compared between sexes, adult females with corpora

lutea to those without, and among ages using a contingency table and log-likelihood ratio statistic (G).

We used Morisita's index (C_λ; Morisita 1959) to examine dietary overlap between sexes, ages, body mass classes (< 2, 2–3.5, > 3.5 kg), fat reserve classes (1 = no fat to 4 = large fat deposits), and female reproductive condition classes (adult females with and without corpora lutea). Morisita's index varies from 0 (no overlap) to 1 (identical diets).

To examine the use of major food groups and different-sized food items, we divided foods into several categories. Mammalian prey was partitioned into size classes: small (*Peromyscus* spp., Short-tailed Shrew [*Blarina brevicauda*], *Sorex* spp., Star-nosed Mole [*Condylura cristata*]), medium (*Rattus* spp., Gray Squirrel [*Sciurus carolinensis*], Red Squirrel [*Tamiasciurus hudsonicus*], Eastern Chipmunk [*Tamias striatus*]), large (Virginia Opossum [*Didelphis virginiana*], Mink [*Mustela vison*], Muskrat [*Ondatra zibethicus*], Snowshoe Hare [*Lepus americanus*], and *Sylvilagus* spp.), and very large (Raccoon [*Procyon lotor*], Striped Skunk [*Mephitis mephitis*], Beaver [*Castor canadensis*], Porcupine [*Erethizon dorsatum*]). White-tailed Deer (*Odocoileus virginianus*) was a separate category of mammalian prey because the majority of its consumption was carrion or bait (Coulter 1966; Powell 1993; Giuliano et al. 1989). Avian prey, which consisted primarily of passerines (Passeriformes) and Ruffed Grouse (*Bonasa umbellus*), were pooled. Fruits, primarily apple (*Malus* spp.), were pooled. We used a contingency table and log-likelihood ratio statistic (G) to examine differences in occurrence of major food groups among Fishers of different age, sex, mass, fat reserves, and reproductive condition.

For all ANOVA, we confirmed homogeneous variances using Levene's test, and normality by plotting data against the expected normal distribution. All tests were performed using SYSTAT software (SYSTAT 1992), and considered statistically significant at $P \leq 0.10$. This value was used, rather than the more common $P \leq 0.05$, to reduce the likelihood of making a Type II error (Zar 1999).

Results

Male Fishers were heavier ($P \leq 0.001$) and had greater fat reserves than females ($P \leq 0.001$; Table 1). Adults were heavier than juveniles among males ($P = 0.001$), but not among females ($P = 0.134$; Table 1). Level of fat reserves was similar among different-aged males ($P = 0.607$) and females ($P = 0.118$; Table 1). Corpora lutea counts ranged from 0–3, and were present only in >1 year old females ($P \leq 0.001$; Table 1). Mean count for females containing ≥1 corporus luteum was 1.83 ± 0.31 ($\bar{x}$ ± SE). Adult females with corpora lutea had similar fat reserves (2.17 ± 0.14; n = 6) to those without corpora lutea (2.65 ± 0.23; n = 19; $P = 0.297$). Adult females with corpora lutea (1.90 ± 0.04 kg) weighed the same as those without (1.83 ± 0.03 kg; $P = 0.719$).

Vermont Fishers consumed 31 different food items. Mammalian food items accounted for 72% of the diet, with 15% avian, and 10% fruit. There were eight food items which were of major importance (>5% occurrence) to either male or female Fishers. Less commonly consumed foods included: Virginia Opossums (*Didelphis virginiana*), Beaver (*Castor canadensis*; assumed to be bait), Mink (*Mustela vison*), moles (*Condylura cristata* and *Parascalops breweri*), voles (*Clethrionomys gapperi* and *Microtus pennsylvanicus*), Woodland Jumping Mice (*Napaeozapus insignis*), lagomorphs (*Sylvilagus* spp. and *Lepus americanus*), *Rattus* spp., Raccoons (*Procyon lotor*), Striped Skunks (*Mephitis mephitis*), invertebrates, fish, reptiles, and amphibians (Table 2).

Diets overlapped considerably between sexes, ages, body mass classes, and fat reserve classes ($C_\lambda > 0.90$), with deer, small mammals, birds, and fruit being the most common food groups (Tables 2, 3, and 4). Use of major food groups did not differ between sexes ($P = 0.883$), ages ($P = 0.836$), body mass classes ($P = 0.640$; Table 3), or fat reserve classes ($P = 0.153$). Diets overlapped considerably (Table 4), and use of major food groups was similar ($P = 0.121$) between adult females with and without corpora lutea.

TABLE 1. Body mass (kg), fat reserves, and reproductive condition (i.e., number of corpora lutea) of Fishers harvested in Vermont, December 1996 (x ± SE).

	Male			Female			
Age	n*	Body Mass	Fat Reserves**	n*	Body Mass	Fat Reserves**	Corpora Lutea***
Juvenile	43	3.18 ± 0.06[a]	3.12 ± 0.12[a]	34	1.77 ± 0.07[a]	2.64 ± 0.12[a]	0 ± 0[a]
Yearling	31	3.82 ± 0.07[b]	3.00 ± 0.13[a]	14	1.77 ± 0.10[a]	2.19 ± 0.19[a]	0 ± 0[a]
Adult	31	4.27 ± 0.07[c]	3.18 ± 0.12[a]	25	1.97 ± 0.08[a]	2.52 ± 0.15[a]	0.48 ± 0.19[b]
All	105	3.76 ± 0.07	3.10 ± 0.07	73	1.84 ± 0.15	2.43 ± 0.09	0.13 ± 0.06

*number of Fishers sampled.
**ocular visceral-fat rank: 1 no fat - 4 large fat deposits.
***corpora lutea counted in right ovary.
[abc]within a column, values followed by the same letter are similar ($P > 0.10$).

TABLE 2. Percent occurrence of food items in Fishers harvested in Vermont, December 1996.

Food Item	Males (n = 115)	Females (n = 82)	Both (n = 197)
White-tailed Deer (*Odocoileus virginianus*)	18.1	15.6	17.1
Avian (mostly passerines)	13.8	15.6	14.6
Peromyscus spp.	9.6	13.3	11.1
Apple (*Malus* spp.)	4.8	9.4	6.7
Muskrats (*Ondatra zibethicus*)	6.4	6.3	6.3
Shrews (*Blarina brevicauda* and *Sorex* spp.)	6.9	3.9	5.7
Squirrels (*Sciurus carolinensis*, *Tamiasciurus hudsonicus*, and *Tamias striatus*)	5.8	4.7	5.1
Porcupines (*Erethizon dorsatum*)	5.3	3.9	4.7
Virginia Oppossums (*Didelphis virginiana*)	3.7	2.3	3.2
Voles (*Clethrionomys gapperi* and *Microtus pennsylvanicus*)	2.7	3.1	2.8
Lagomorphs (*Lepus americanus* and *Sylvilagus* spp.)	3.7	1.6	2.8
Fish	1.6	1.6	1.6
Beavers (*Castor canadensis*)	1.6	0.7	1.3
Mink (*Mustela vison*)	1.1	1.6	1.3
Invertebrates	0.5	1.6	0.9
Moles (*Condylura cristata* and *Parascalops breweri*)	0.5	0.8	0.6
Woodland Jumping Mice (*Napaeozapus insignis*)	0.5	0.8	0.6
Reptiles and Amphibians	1.1	0.0	0.6
Raccoons (*Procyon lotor*)	0.5	0.0	0.3
Striped Skunks (*Mephitis mephitis*)	0.0	0.8	0.3
Rattus spp.	0.0	0.8	0.3

Discussion

We found Fishers to have a diverse diet with the most utilized dietary items during late fall being White-tailed Deer, birds, and small mammals. These findings are similar to those of other studies of Fisher food habits in eastern North America (*see* Douglas and Strickland 1987; Martin 1994; Powell and Zielinski 1994 for reviews) that found Fishers to be opportunistic feeders. Consumption of deer was probably the result of scavenging or use of baits, and appears to be an important dietary component of Fishers in northeastern North America (Coulter 1966; Kelly 1977; Rego 1984; Giuliano et al. 1989). However, unlike Coulter (1966), Leonard (1980), Powell (1993), and Raine (1987), who found Snowshoe Hare to be a frequently used food, we found Snowshoe Hare to contribute little to Fisher diets. Further, in contrast to Fishers in Manitoba (Raine 1987), our results suggest that birds and small mammals are important prey, as did numerous other studies (*see* Douglas and Strickland 1987; Martin 1994; Powell and Zielinski 1994 for reviews). Where their ranges overlap, Porcupines are often a major prey of Fishers, composing as much as 34% of the diet in some studies (deVos 1952; Rego 1984; Powell 1993). Although Porcupines were consumed in Vermont, they were consumed less than reported levels. The differences in findings among studies

TABLE 3. Percent occurrence of major food groups in Fishers harvested in Vermont, December 1996.

	Fisher Age			Fisher Body Mass (kg)		
Food Item	Juvenile (n = 77)	Yearling (n = 44)	Adult (n = 55)	<2 (n = 65)	2–3.5 (n = 56)	>3.5 (n = 72)
White-tailed Deer (*Odocoileus virginianus*)	24.7	27.3	30.9	15.4	15.4	19.4
Small mammal[a]	48.1	47.7	41.8	33.0	28.2	25.9
Medium mammal[b]	6.5	13.6	9.1	6.3	5.2	4.6
Large mammal[c]	23.4	18.2	18.2	11.4	12.0	8.3
Very large mammal[d]	11.7	4.6	12.7	4.6	6.8	17.9
Fruit (mostly apple [*Malus* spp.])	14.3	11.4	2.0	8.0	15.4	7.4
Avian (mostly passerines)	27.3	15.9	25.5	18.2	12.8	13.9

[a]*Peromyscus* spp., *Blarina brevicauda*, *Sorex* spp., and *Condylura cristata*.
[b]*Rattus* spp., *Sciurus carolensis*, *Tamiasciurus hudsonicus*, and *Tamias striatus*.
[c]*Didelphis virginiana*, *Ondatra zibethicus*, *Lepus americanus*, *Sylvilagus* spp., and *Mustela vison*.
[d]*Procyon lotor*, *Mephitis mephitis*, *Castor canadensis*, and *Erethizon dorsatum*.

TABLE 4. Dietary overlap (C_λ) of Fishers of different sex, age, body mass, fat reserves, and between females with and without copora lutea, harvested in Vermont, December 1996.

Comparison	C_λ*
Male vs. Female	1.00
Juvenile vs. Yearling	0.97
Juvenile vs. Adult	0.98
Yearling vs. Adult	0.97
Body Mass: <2 kg vs. 2–3.5 kg	0.98
Body Mass: <2 kg vs. >3.5 kg	0.93
Body Mass: 2–3.5 kg vs. >3.5 kg	1.00
Fat Reserve Class** 1 vs. 2	0.92
Fat Reserve Class 1 vs. 3	0.95
Fat Reserve Class 1 vs. 4	0.98
Fat Reserve Class 2 vs. 3	0.98
Fat Reserve Class 2 vs. 4	0.96
Fat Reserve Class 3 vs. 4	0.99
Females With Corpora Lutea vs. Females Without Corpora Lutea	1.00

*Morisita's index (C_λ) varies from 0 (no overlap) to 1 (identical diets)
**Ocular visceral-fat rank: 1 no fat – 4 large fat deposits.

were likely the result of differences in prey species availability, diversity, and quality (i.e., caloric and nutrient value) among regions and periods (Leonard 1980; Raine 1987; Giuliano et al. 1989; Thompson and Colgan 1990). However, data to address these possibilities were not available.

Our finding that male and female Fishers had highly similar diets was similar to that of Coulter (1966), Kelly (1977), Giuliano et al. (1989), and Powell (1993), but contrary to the general prediction of Brown and Lasiewski (1972; supported by Powell and Leonard 1983) who suggested that mustelids evolved intersexual differences in body size to reduce intraspecific competition for food. Use of different foods and foods of different size by Fishers of different ages and size also could reduce intraspecific competition. However, we found that fall diets did not differ by Fisher age or size. In nearby New Hampshire, Giuliano et al. (1989) found that large males consumed more White-tailed Deer and apples than did females. They suggested this was because males used larger home-ranges than females, increasing their encounters with these foods, and because males denied smaller females access to these concentrated foods. However, neither our data nor that of Kelly (1977) support this conclusion.

Only adult (≥2 yrs) females had corpora lutea, which probably reflects increased fertility of Fishers with age (Leonard 1986). Females with corpora lutea had fewer (mean = 1.8) than have been found for females in other studies (range 2.7–3.7; Eadie and Hamilton 1958; Wright and Coulter 1967; Shea et al. 1985; Leonard 1986). Other studies have also documented females with corpora lutea as yearlings (Eadie and Hamilton 1958; Shea et al. 1985; Leonard 1986). The reason for lower corpora lutea counts in Vermont Fishers is not clear. Adult Fishers with and without corpora lutea had the same level of fat, suggesting that condition was not a limiting factor. Further, we found that reproductive condition was not a function of diet or body mass among adults during late fall. It is possible that during late winter, when food resources are presumably more limiting, and during spring, when the energy demands of reproduction increase dramatically (Powell and Leonard 1983), that female Fisher reproductive condition and fat reserves may be influenced by diet.

Land management practices that promote a diversity of habitats, and thus prey, should be advocated as a conservation strategy for species such as Fisher, capable of utilizing a variety of prey. Of particular concern are anti-logging initiatives and the suppression of disturbance factors (e.g., fire, pest outbreaks) that reduce the availability of early successional habitats important to numerous prey (e.g., deer, lagomorphs, grouse, and many small mammals). Fishers in Vermont and elsewhere exhibit age-specific fecundity, with older animals having greater fecundity. Thus, if older females are more vulnerable to harvest or otherwise underrepresented in the population, management to reverse this trend may be needed.

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Relative Abundances of Forest Birds of Prey in Western Newfoundland

JOHN W. GOSSE[1], and WILLIAM A. MONTEVECCHI[2]

[1]Terra Nova National Park, Glovertown, Newfoundland, A0G 2L0, Canada
[2]Biopsychology Programme, Psychology and Biology Departments, Memorial University of Newfoundland, St. John's, Newfoundland, A1B 3X9, Canada

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We surveyed woodland birds of prey in different-aged Balsam Fir (*Abies balsamea*) forests in western Newfoundland. Nine species of birds of prey were recorded: Merlin, American Kestrel, Osprey, Rough-legged Hawk, Sharp-shinned Hawk, Northern Goshawk, Boreal Owl, Great Horned Owl and Northern Hawk-Owl. Playback broadcasts generated low response rates but did facilitate most detections of nocturnal owls and rarer birds of prey. Numbers of birds of prey were low but were highest and most diverse in old-growth forests. Clearcuts provided habitat for open-nesting raptors (hawk-owls, kestrels and in one year Rough-legged Hawks). Owing to rarity of woodland raptors in western Newfoundland, we recommend that large expanses of late-successional forest be set aside for the conservation of birds of prey and other wildlife.

Key Words: Birds of prey, Newfoundland, broadcast surveys, habitat associations, relative abundance.

Extensive research describing habitat associations of woodland birds of prey has been conducted in North America and Europe (Titus and Mosher 1981; Armstrong and Euler 1982; Reynolds et al. 1982; Hayward et al. 1993; Solonen 1994). Though patterns of habitat use have emerged, results are often site-specific and vary greatly across the geographic ranges of some species. Breeding densities of birds of prey are generally assumed to be limited by either an adequate food source, the number and distribution of suitable nesting sites, or some combination of these factors (Newton 1979). Furthermore, these factors likely vary within and between species and across different temporal and spatial scales. Monitoring the densities of wildlife populations (number of individuals or pairs/area) is of interest to ecologists and managers when assessing the potential environmental impacts of land-use practices. Habitat quality can be partially assessed by determining the number of individuals that inhabit an area, though the validity of using breeding density as the only or most important indicator of habitat quality has been questioned (Van Horne 1983). Though numerous raptor surveys have been conducted across North America, surveys are typically localized and feature more easily detected species in open habitats (Schmutz 1984; Andersen and Rongstad 1989). Density estimates are difficult to obtain for woodland species during the breeding season because they are typically wide-ranging, secretive and often nest in inaccessible areas, particularly in northern boreal forests (Fuller and Mosher 1987).

The boreal forest of insular Newfoundland constitutes the extreme eastern and southern limits of the ranges of many North American woodland raptors. The requirement for research on forest birds of prey in this region is necessary since this landscape has been drastically altered by forest harvesting resulting in extensive fragmentation and a shift in the age-class distribution of the forest. Habitat loss from timber harvesting is recognized as a serious threat to populations of some woodland raptors (Armstrong and Euler 1982; Carey et al. 1990; Crocker-Bedford 1990), yet on insular Newfoundland, guidelines for managing woodland raptors are inadequate and, prior to this research, the consequences of forest removal on raptor ecology had not been considered. Large scale commercial forest harvesting is intensive in Newfoundland (Thompson et al. 1999) thus, it is important to investigate the species composition and relative abundances of birds of prey in different forest habitats to assess how forestry practices may influence raptor diversity and abundance. In this study we surveyed the diversity, distribution, and abundance of woodland birds of prey in different-aged balsam fir forests in western Newfoundland.

Study Area and Methods

The Western Newfoundland Model Forest (WNMF) study area (707 000 ha) occurs within the Corner Brook subregion of the Western Forest Ecoregion of insular Newfoundland (Damman 1983). This subregion is characterized by hilly terrain up to 600 m above sea level. Forests are primarily Balsam Fir with occasional with White Spruce (*Picea glauca*), Black Spruce (*P. mariana*) and White Birch (*Betula papyrifera*; Newfoundland Forest Service 1992). The humid climate minimizes

fires (Damman 1983), and under natural conditions infestations of Hemlock Looper (*Lambdina fiscellaria*) and Spruce Budworm (*Choristoneura fumiferana*) are responsible for forest renewal in western Newfoundland (Bazukis and Hansen 1965). Defoliated patches of forest and clear-cuts from timber removal for pulp have resulted in a very fragmented landscape in this region. We classified "uncut old-growth" as forest greater than 80 years old that has never been commercially harvested. Small forest openings (~100 × 100 m) resulting from insect defoliation, and an abundance of snags and coarse woody debris typify these sites. Tree heights often reach 20–24 m (Newfoundland Forest Service1992). Second-growth forests in western Newfoundland are 40 to 60 year old regenerated stands that originated following timber harvesting earlier in the 20th century. Compared with uncut older forests, these stands are characterized by smaller tree diameters, more stems/hectare, higher shrub diversity and less woody debris (Thompson and Curran 1995). Clear-cut sites resulting from forest harvesting have had most of the wood volume removed, though some deciduous and otherwise unmerchantable trees remain on these sites. Herbaceous ground vegetation consisting of raspberry (*Rubus* spp.) and alder (*Alnus* spp.) is dense; however some clear-cuts are devoid of most ground vegetation owing to treatment with herbicides. Clear-cuts range from 5 to15 years old. Pre-commercially thinned areas are found throughout the study area and range from 10–30 years old. These regenerating sites have been artificially thinned to promote more efficient tree growth and are composed mainly of Balsam Fir.

Study sites within the WNMF were established in uncut old-growth, second-growth, pre-commercially thinned areas and clear-cuts, and were located near Little Grand Lake, George's Lake and Cook's Pond, respectively (Figure 1). In 1993, seven transects passing through uncut old-growth, second-growth, clear-cuts and pre-commercially thinned areas were established along forest roads. In areas inaccessible by truck, an all-terrain vehicle or boat was used to access the transects. However, because of the relative inaccessibility of old-growth sites and the time constraints for surveying during the breeding season, habitats were not sampled relative to their availability. Each transect was surveyed three times for the target species during the breeding season (Table 1). Survey stations were set up at 800 m intervals along the transects. At each survey station, territorial vocalizations were broadcast to elicit responses from territorial adults that could occur in the area (Mosher et al. 1990). In 1993, the target species were Sharp-shinned Hawks (*Accipiter striatus*), Northern Goshawks (*A. gentilis*), Merlins (*Falco columbarius*), Boreal Owls (*Aegolius funereus*) and Great Horned Owls (*Bubo virginianus*). A battery powered Realistic vsc-2001 cassette recorder and two Realistic portable Minimus-

FIGURE 1. The western Newfoundland Model Forest Study area (shaded region). Study sites are indicated by numbers 1–3.

0.6 speakers (83 db/1m) were used for the playbacks. Recordings were obtained from the Cornell Laboratory of Ornithology and from the Peterson Field Guide Series (Myer and Peterson 1990). Surveys were not conducted during periods of inclement weather; i.e. heavy fog, prolonged rain, or winds greater than Beaufort 3 (13–19 km/h; Mosher et al. 1990).

Upon arriving at each survey station, observers would listen and look for birds of prey for 1 min. Then, a series of six 20-sec playbacks of a single species' vocalizations, separated by 30 sec silent intervals, were made during a 5-min period. Three vocalization segments were broadcast toward an arbitrarily selected side of the road (determined by coin toss), followed by three broadcast segments to the other side. The observer would then remain at the site for an additional 5 min to listen and look for birds of prey. Diurnal species were identified from vocalizations, flight characteristics and plumage patterns, and nocturnal owls from auditory cues. Birds were considered territorial adults if repeatedly recorded at the same site, if an aggressive response was elicited by the observer, or if fledglings were seen late in the breeding season. Unconfirmed sightings of raptors were not included in the analyses. Only one target species was surveyed on any morning or night. Playbacks for the remaining target species were broadcast on successive days. Nocturnal surveys were conducted from 22:30 to 02:00, and morning surveys from 06:00 to 10:00. The survey period in 1993 was from 24 May to 14 August. Birds observed between survey stations

TABLE 1. Survey transect specifications for the four forest types in western Newfoundland, 1993–1994.

Forest Habitat Type	Number of transects	Transect lengths (km)	Number of broadcast stations	Surveyed area (km^2)
1993				
Uncut old-growth	2	15	19	18.0
Second growth	1	9	11	10.8
Thinned	2	18	22	28.8
Clearcut	2	16	20	25.6
Total	**7**	**58**	**72**	**83.2**
1994				
Uncut old-growth	3	18	22	21.6
Second growth	2	16	20	19.2
Clearcut	2	16	20	25.6
Total	**7**	**50**	**62**	**66.4**

were recorded to the nearest station from the point of contact.

In 1994, survey routes were re-established to ensure that distances surveyed in each habitat type were comparable. The distances surveyed in uncut old-growth, second growth and clear-cut areas were 18, 16 and 16 km respectively, and an equal number of surveys (n = 3) were conducted along each route. Pre-commercially thinned areas were not surveyed in 1994 because the total area of this habitat type in the WNMF is negligible and therefore of less interest. Playbacks for Merlins were not broadcast in 1994, because results from 1993 indicated that they did not respond to broadcast vocalizations. Broadcast surveys using vocal recordings of Sharp-shinned Hawks, Northern Goshawks, Boreal Owls, Great Horned Owls and Northern Hawk-Owls (*Surnia ulula*) were run from 1 June to 15 August 1994. In contrast to the methods used in 1993, individual surveys involved playbacks for multiple species on each outing. That is, nocturnal surveys involved broadcasting playbacks for each owl species at every second 800-m interval along the survey route. Lack of response due to habituation to the playbacks was considered minimal since only three visits were made to each point during the season. Playbacks for individual diurnal species were broadcast at every third 800-m interval along survey routes. Broadcasting for multiple species on each survey controlled for variations in weather conditions that might otherwise influence detectability when individual species broadcasts were run on successive days. Further, surveys were initiated at alternating ends of survey routes on successive visits to balance the potential effect of varying broadcast times. We also ensured that vocalizations of the target species were broadcasted at each survey station during the breeding season. In March 1995, 26 km of uncut old-growth forest was surveyed for Boreal and Great Horned Owls using playbacks. Broadcast stations were 800 m apart and access was by snowmobile.

The area surveyed in each habitat type was calculated by multiplying the km driven on forest roads and lake shorelines by the estimated distance on each side of the route to which broadcasts were audible. Mosher et al. (1990) found that broadcasts with a comparable db output were audible to humans at 750 m away from the source in a hardwood stand in Maryland. In this study, the distance that broadcasts were still audible to researchers was estimated to be 600 m in forest habitats and 800 m in clearcuts and pre-commercially thinned areas.

The numbers of each species in each habitat were compiled and compared using a non-parametric randomization technique (Manly 1991). The randomization test is a re-sampling procedure which creates its own frequency distribution based on the original abundance data, thus eliminating the assumptions of normality (Adams and Anthony 1996). The measure used for the among-habitat comparisons was the number of birds/km averaged over all visits to that station. In the initial step of the randomization test, the difference between the observed mean values of raptors/broadcast station between the two habitats being compared was calculated. A frequency distribution of 3000 possible outcomes of differences between the mean values was then randomly generated with replacement from the original data. Habitats are significantly different with respect to the number of birds/km if the observed difference of mean values between the two habitats lies outside the 95% confidence interval set around the distribution of 3000 possible mean outcomes.

Results

Effectiveness of vocalization broadcasts

Seven transects totalling 58 and 50 km (habitats combined) were surveyed for woodland birds of prey in 1993 and 1994, respectively (see Table 1). Although responses of raptors to the broadcast vocalizations were elicited on occasion, most sightings occurred while driving between broadcast sta-

tions or before the calls were broadcast. In 1993, only three of 94 birds detected (3.2 %) were in response to broadcast vocalizations. Two of these were Boreal Owls and the other a Sharp-shinned Hawk. In 1994, 8 of 105 raptors detected (7.6 %) were in response to broadcast vocalizations, these included Sharp-shinned Hawks (2), Great Horned Owls (2), Northern Hawk-Owls (3), and a Boreal Owl. It is notable that when responses to broadcasts did occur, they were elicited during the 5-min broadcasting period. Numbers for both years were not combined because of differences in the survey methodologies used during each breeding season.

Species composition

Nine species of raptors were recorded within the study area during 1993 and 1994: Merlin, American Kestrel (*Falco sparverius*), Osprey (*Pandion haliaetus*), Rough-legged Hawk (*Buteo lagopus*), Sharp-shinned Hawk, Northern Goshawk, Boreal Owl, Great Horned Owl, and Northern Hawk-Owl (see Table 2).

Relative abundances and habitat associations of birds of prey

Uncut old-growth Balsam Fir forests near Little Grand Lake were used by Sharp-shinned Hawks, Merlins, Boreal Owls and Ospreys in 1993 and 1994, and a Northern Goshawk in 1994. The number of territorial adults and the number of birds/km for each species by habitat and year are given in Table 3. Although numbers are low, indices of relative abundances are derived. In 1993, Sharp-shinned Hawks and Boreal Owls were the most abundant species (birds/km for these species were 0.27 and 0.33, respectively). Merlins and Ospreys were less abundant along survey routes through this habitat at 0.07 and 0.13 birds/km, respectively. In 1994, Sharp-shinned Hawks were only found in old-growth forest at a density of 0.22 birds/km. A comparison of Merlin numbers between years was not made because of differences in the surveying methodology used in each season. Only one Boreal Owl was detected in 1994 compared with five the previous year. In addition, the only goshawk recorded during this study occurred in uncut old-growth forest in 1994.

In 1993, 9 km of this habitat was surveyed resulting in only one sighting of each of these species. In 1994, vocalizations broadcast along 16 km of second-growth forest near George's Lake resulted in four Merlin and two Great Horned Owl detections (Table 3). Three species of woodland raptors were identified along survey routes transecting second-growth forests near Victoria Lake and George's Lake: Sharp-shinned Hawk, Merlin, and Great Horned Owl. In addition to the focal species, second-growth forests in various successional stages were utilized by an estimated 20 nesting pairs of Osprey in the Stephenville Crossing area.

Clear-cuts provided nesting and foraging habitat for both Northern Hawk-Owls (two nests) and American Kestrels (two nests) as well as foraging sites for Merlins and Rough-legged Hawks. In 1993, birds/km ranged from 0.13 for Rough-legged Hawks to 0.19 birds/km for Merlins and Northern Hawk-Owls. In 1994, Rough-legged Hawks were not sighted in clear-cuts; however, two American Kestrels were recorded (0.13 birds/km). Merlin were recorded at a density of 0.19 birds/km (Table 3). In 1993, surveys along 18 km of pre-commercially thinned areas indicated that only Rough-legged Hawks (0.17 birds/km) and Merlins (0.06 birds/km) used these areas for foraging (Table 3). No species were known to utilize thinned areas for nesting. Owls were not detected along 26 km of uncut old-growth forest in March 1995. Old-growth Balsam Fir forests were utilized by more species than the other forest types, though habitats did not differ significantly with respect to the mean number of birds/km recorded along the survey routes.

TABLE 2. Sightings and habitat associations of adult birds of prey in western Newfoundland, 1993–1994. Numbers also include birds of prey recorded in areas outside of survey routes but in the WNMF region.

Species	Number of sightings (estimated number of individuals) 1993	1994	Total	Balsam Fir habitat type
Merlin	25 (14)	22 (16)	47 (30)	Clear-cuts, old and young second growth, uncut old-growth
American Kestrel	9 (8)	4 (4)	13 (12)	Clear-cuts
Osprey	5 (4)	35 (24)	40 (28)	Young second growth and uncut old-growth near large water bodies
Rough-legged Hawk	22 (18)	0 (0)	22 (18)	Barren, clear-cuts, cliffs
Sharp-shinned Hawk	13 (6)	15 (8)	28 (14)	Uncut old-growth, old second growth
Northern Goshawk	0 (0)	4 (1)	4 (1)	Uncut old-growth
Boreal Owl	8 (5)	1 (1)	9 (6)	Uncut old-growth
Great Horned Owl	2 (2)	8 (4)	10 (6)	Old second growth
Northern Hawk-Owl	10 (5)	14 (7)	24 (12)	Clear-cuts

TABLE 3. Number of birds of prey/km detected along survey routes in different Balsam Fir forest types in western Newfoundland, 1993–1994. Numbers of individuals in parentheses do not include repeat sightings. Species name abbreviations: M = Merlin, K = American Kestrel, O = Osprey, RLH = Rough-legged Hawk, SSH = Sharp-shinned Hawk, GH = Northern Goshawk, B = Boreal Owl, GHO = Great Horned Owl, NHO = Northern Hawk-owl.

Habitat type	Km	Birds/km										# of
1993	surveyed	M	K	O	RLH	SSH	GH	BO	GHO	NHO	Overall	species
Uncut old-growth	15	0.07 (1)	0	0.13 (2)	0	0.27 (4)	0	0.33 (5)	0	0	0.80 (12)	4
Second-growth	9	0.11 (1)	0	0	0	0.11 (1)	0	0	0.11 (1)	0	0.33 (3)	3
Clear-cut	16	0.19 (3)	0	0	0.13 (2)	0	0	0	0	0.19 (3)	0.51 (8)	3
Thinned	18	0.06 (1)	0	0	0.17 (3)	0	0	0	0	0	0.23 (4)	2
1994												
Uncut old-growth	18	0.17 (3)	0	0.11 (2)	0	0.22 (4)	0.06 (1)	0.06 (1)	0	0	0.62 (11)	5
Second-growth	16	0.25 (4)	0	0	0	0	0	0	0.13 (2)	0	0.38 (6)	2
Clear-cut	16	0.19 (3)	0.13 (2)	0	0	0	0	0	0	0.19 (3)	0.51 (8)	3

Discussion

Woodland birds of prey generally occur in low densities, are secretive, wide-ranging, and therefore difficult to census (Fuller and Mosher 1981). In light of this, broadcasting taped calls as a means of improving detection rates, and hence estimating bird densities, has become an increasingly prevalent technique for detecting forest raptors. This method has been used to increase detection rates of Spotted Owls (*Strix occidentalis*) (Forsman et al. 1977), Red-shouldered Hawks (*Buteo lineatus*), Cooper's Hawks (*Accipiter cooperii*), Barred Owls (*Strix varia*) (Mosher et al. 1990) and Northern Goshawks (Kennedy and Stahlecker 1993). Four species of birds of prey responded to taped broadcasts in our study area. Although not highly effective in the present study, (only 3 and 8 % of the total detections of woodland raptors in 1993 and 1994, respectively), playbacks accounted for two of three Great Horned Owl detections, three of six Boreal Owl and Northern Hawk-owl detections, and one of nine Sharp-shinned Hawk detections. We speculated that responses to vocalizations and hence the abundance estimates of Boreal and Great Horned Owls might have been higher in late winter or early spring (February–April) when territories are being established (Morrell et al. 1991; Hayward et al. 1993). To test this, we conducted surveys for these species in uncut old-growth forest during 15–21 March 1995; however, no owls were detected. Lundberg (1979) found that "territorial and breeding pairs of Boreal Owls were more silent than non-territorial individuals," so censuses using playbacks may give biased estimates of owl abundances and may not be sensitive for detecting breeding pairs. Hayward et al. (1993) contended that a lack of understanding of the factors that affect Boreal Owl singing rates makes the vocalization method an inappropriate monitoring tool. Hence, censusing birds of prey in forested habitats remains problematic, and research is needed to develop more reliable and robust censusing techniques.

Surveys conducted during the 1993 and 1994 breeding seasons indicated that uncut old-growth forest contained the most individuals and the most species. Forests in advanced stages of natural succession in western Newfoundland are typified by extensive snag retention and stands are of various ages, thus allowing a potentially wider range of species to inhabit this habitat type. Boreal Owls, for example, require tree cavities for nesting (Hayward et al. 1993) and were restricted to uncut old-growth Balsam Fir forests. Sharp-shinned Hawks prefer a dense canopy cover for nesting (Moore and Henny 1983) and a relatively open understory for hunting, and were found mainly in old-growth forests.

Second-growth forests in Newfoundland are younger even-aged forests (Thompson and Curran 1995) with less structural diversity than uncut old-growth forests. They supported fewer species than uncut old-growth forests. Surveys in second-growth forests indicated the presence of only three species of birds of prey, one of which, Great-Horned Owl, is considered a habitat generalist with a wide ecological tolerance (Bosakowski et al. 1989).

Clear-cuts provided breeding and feeding habitat for Northern Hawk-Owls and American Kestrels. Large hardwood snags have been left intact throughout these areas providing both nesting structures and perching sites for foraging. Merlins were also frequently observed hunting in this habitat as were

Rough-legged Hawks in 1993. The latter species is an aerial predator which prefers open ground, although typically at more northerly tundra habitats (Poole and Bromley 1988; Whitaker et al. 1996).

Recommendations for the management of birds of prey in western Newfoundland

Birds of prey have received increasing attention with respect to land-use decisions in recent decades. Human development has led to a general decline in birds of prey on a global scale. Three main factors have been identified as causing declines (or limiting numbers): destruction and degradation of habitat, persecution by humans, and contamination by toxic chemicals (Newton 1979). The standard method of timber harvesting in western Newfoundland is clear-cutting. This method may be the most economical in terms of obtaining large amounts of timber, however it creates large areas of unsuitable habitat for forest birds of prey that are dependent on older age classes. Alternative harvesting techniques should be explored to ensure the continued existence of wildlife populations in regions with intensive forest utilization. Different silvicultural techniques may influence raptor populations in various ways thus it is critical to determine which species of birds of prey and other species are to be given priority in forestry management plans. Though none of the woodland birds of prey observed in this study are listed by the Committee for the Status of Endangered Wildlife in Canada [COSEWIC] (Kirk and Hyslop 1998), we propose that species primarily associated with mature and uncut old-growth Balsam Fir forest (Northern Goshawks, Boreal Owls and Sharp-shinned Hawks), be featured in management programs because the distribution of this age class in western Newfoundland has been greatly reduced, and further habitat loss would likely have negative impacts on the resident species (Thompson et al. 1999; Setterington et al. 2000). Woodland raptors occur in low numbers, and it is necessary to preserve large expanses of adequate habitat in order to provide for viable populations. Conservation of older forests would also benefit other wildlife species such as American Marten (*Martes americana atrata*) and some forest birds (see Whitaker and Montevecchi 1997, 1999; Thompson et al. 1999).

Forest harvesting may also have inadvertently increased the amount of habitat available to certain species that prefer open habitats and consequently resulted in an expansion of their ranges or an increase in their populations. For example, Northern Hawk-Owls and American Kestrels utilized clearcuts for nesting and foraging. The American Kestrel's range has expanded into Newfoundland since the 1940s, or at least its numbers appear to have increased (Montevecchi and Tuck 1987). Foraging raptors that use pause-travel-search tactics (i.e., Northern Hawk-Owls) have been documented to use clearcuts with perches significantly more frequently than clear-cuts lacking perches (Widen 1994). Habitats for cavity-dependent species such as Boreal Owls and American Kestrels may also be potentially expanded or improved by establishing nest-box programs, especially in younger successional forests where suitable nesting cavities are lacking. Such programs would be relatively inexpensive and could also provide valuable and much-needed public education concerning forest birds of prey and wildlife conservation.

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Distances Moved by Small Woodland Rodents within Large Trapping Grids

JEFF BOWMAN[1, 3], GRAHAM J. FORBES[2], and TIM G. DILWORTH[1]

[1]Department of Biology, University of New Brunswick, P. O. Box 45111, Fredericton, New Brunswick E3B 6E1, Canada
[2]New Brunswick Cooperative Fish and Wildlife Research Unit, P. O. Box 44555, Fredericton, New Brunswick E3B 6C2, Canada
[3]Present address: Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada

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During a four-year study in New Brunswick, Canada, we documented long-distance movements (> 125 m) for three small-mammal species. Individuals from every species studied made long-distance movements, but relative to abundance, more Woodland Jumping Mice moved than any other species (9.4% of captures). Mean straight-line distances moved were: 370 m (Deer Mice, *Peromyscus maniculatus*; N = 44), 225 m (Woodland Jumping Mice, *Napaeozapus insignis*; N = 33), and 224 m (Red-backed Voles, *Clethrionomys gapperi*; N = 23). Frequency of movement decreased with distance for all species. The study demonstrated that long-distance movements were not uncommon, and as such, they may be an important component of the population dynamics of small mammals.

Key Words: Red-backed Vole, *Clethrionomys gapperi*, Deer Mice, *Peromyscus maniculatus*, Woodland Jumping Mouse, *Napaeozapus insignis*, movement, scale dispersal, New Brunswick.

Movement contributes to temporal and spatial structure of populations (Wiens et al. 1993). Empirical descriptions of movements for small mammals are rare, in part, because of the methods used to sample populations (Howard 1960; Clark et al. 1988). Trapping grids frequently are too small in spatial extent to detect long-distance movements (e.g., Burt 1940; Smith et al. 1975; Wegner and Merriam 1990; Merriam 1995). There are, however, scattered reports of long-distance movements for a variety of small-mammal species, for example: Deer Mice, *Peromyscus maniculatus* (Howard 1960; Bowman et al. 1999), White-footed Mice, *Peromyscus leucopus* (Krohne et al. 1984; Wegner and Merriam 1990), Woodland Jumping Mice, *Napaeozapus insignis* (Ovaska and Herman 1988), Stephens' Kangaroo Rats, *Dipodomys stephensi* (Price et al. 1994), Western Harvest Mice, *Reithrodontomys megalotis* (Clark et al. 1988), and observations of several species described in Kozakiewicz and Szacki (1995). These reports are an important source of data which can help ecologists to understand the process of dispersal (e.g., Kozakiewicz and Szacki 1995; Sutherland et al. 2000). For example, dispersal distance is frequently a component of spatially-explicit simulation models (e.g., Pulliam et al. 1992; Wilson et al. 1993; With and Crist 1995), and such models can be parameterised with empirical dispersal data.

During a four-year study of the spatial structure of small-mammal populations in a managed forest in New Brunswick, Canada, the study design involved large (4900 ha) live-trapping grids and provided an opportunity to assess long-distance movements for three species. Here, we describe the magnitude, variability, and seasonality of long-distance movements made by: *Peromyscus maniculatus*, *Napaeozapus insignis*, and Red-backed Voles, *Clethrionomys gapperi*.

Methods

The study took place in the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of Sugar Maple (*Acer saccharum*), Yellow Birch (*Betula alleghaniensis*), and American Beech (*Fagus grandifolia*). Lowland sites were dominated by Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), and Balsam Fir (*Abies balsamea*).

The study design was described in detail by Bowman et al. (2000). Two 4900-ha forested landscapes with contrasting management intensities (> 50% clearcuts or plantations < 15 yrs old vs < 15% clearcuts or plantations < 15 years old) were systematically live-trapped using a set of nested grids. The two largest grids (one per landscape) had grains (or distance between sampling points) of 1000 m and areal extents of 4900 ha (8 × 8; 64 points in each grid). Nested within each of the large grids was a smaller grid with a grain of 250 m and an extent of 310 ha (8 × 8; 64 points in each grid), and on the less intensively-managed landscape, there was a third grid with a grain of 125 m and an extent of 31 ha (5 × 6; 30 points). A total of 260 sample points were spread systematically across the two

landscapes within these grids. At each point an array of five Victor Tincat multiple-capture live traps (Woodstream Corp., Lititz, Pennsylvania, USA) was used to sample small-mammal populations. Traps were placed at point centre and 35-m from the centre on each compass ordinal; each trap was placed in a "most likely runway" position. Traps were prebaited for three days with oats and sunflower hearts and then set for four consecutive nights. The trapping protocol was carried out twice per annum in spring (May–June) and fall (August–September). Captured animals were weighed, identified to species and gender, checked for reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, Kansas, USA) and released. Our protocol was approved by the University of New Brunswick Animal Care Committee.

We considered that an animal had moved if it was recaptured (i.e., with an ear tag) at a sample point where it had not been captured previously. The finest grain in our study was 125 m (i.e., the space between sample points on the 31 ha trapping grid) so 125 m was our definition of a long-distance movement. Shorter movements were not long enough to move an animal between sample points, and were not considered in our analysis. Movement distances were calculated as straight-line distances between the centres of the capture and recapture sample points. Calculations were made using digital maps of the study area and a Geographic Information System (GIS; Arc/View).

We used nonparametric analyses to compare distances moved by different species, and where sample sizes were suitable, to compare distances moved by sex and age groups within species. We calculated the relative frequencies of long-distance movements by different species, and within-species seasonal differences in the number of captures after long-distance movements.

Results

The three most abundant rodents captured were Red-backed Voles (9.40 captures/100 trap nights), Deer Mice (7.66 captures/100 tn), and Woodland Jumping Mice (2.78 captures/100 tn). These three were the only species for which long-distance movements were observed. Relative to abundance and combining seasons, more Woodland Jumping Mice moved between sampling points than any other species: 9.4% of captures occurred after long-distance movements, compared to 4.2% and 1.8% for Deer Mice and Red-backed Voles, respectively (Table 1). These proportions were calculated by omitting captures on the two largest (1000-m grain) grids, because no movements were ever recorded at this largest scale.

There were no differences in distances moved by males, females, or juveniles within any species. Thus, we combined within-species sex and age classes to compare distances moved by different species and found that Deer Mice moved farther than either of the other species ($\chi^2 = 5.9$, df = 2, P = 0.048) (Figure 1, Table 1). Sample sizes were too small to assess within-species, age- and sex-related statistical patterns in seasonal movements. However, by combining ages and sexes and controlling for trap effort, we found that Deer Mice ($\chi^2 = 4.5$, df = 1, P = 0.035) and Red-backed Voles ($\chi^2 = 7.4$, df = 1, P = 0.007) were more frequently captured in fall than in spring, after having moved a long distance. Conversely, Woodland Jumping Mice were more frequently captured in spring than in fall, after having moved a long distance ($\chi^2 = 8.76$, df = 2, P = 0.003) (Table 1).

Discussion

Individuals from all three of the abundant species in our study area moved distances in excess of 125 m. The frequency of movements generally decreased with distance, which is consistent with studies of dispersal across a range of taxa (Taylor 1980; Sutherland et al. 2000).

Deer Mice made longer movements than either Red-backed Voles or Woodland Jumping Mice — the longest of these (1768 m) was reported by Bowman et al. (1999). Other authors have recognised the ability of Deer Mice (and closely-related White-footed Mice) to move long distances. Howard (1960) recorded a movement of 1000 m for *P. maniculatus*, and Wegner and Merriam (1990) speculated about movements by *P. leucopus* of > 1000 m. While Ovaska and Herman (1988) demonstrated a movement by a Woodland Jumping Mouse of > 800 m, we are unaware of other studies reporting

TABLE 1. Distances (m) moved by small woodland rodents within large trapping grids in New Brunswick, Canada, during 1997–1999.

Species	Mean	SE	Max	N (S, F)[A]	Rate (%)[B]	J[C]	F[D]	M[E]
Peromyscus maniculatus	370	55	1768	44 (15, 29)	4.2	23	7	14
Napaeozapus insignis	225	22	607	33 (25, 8)	9.4	3	10	20
Clethrionomys gapperi	224	24	494	23 (5, 18)	1.8	13	1	9

[A]Total number (number in spring, number in fall)
[B]Percentage of captures that had moved > 125 m.
[C]Number of juveniles and subadults
[D]Number of adult females
[E]Number of adult males

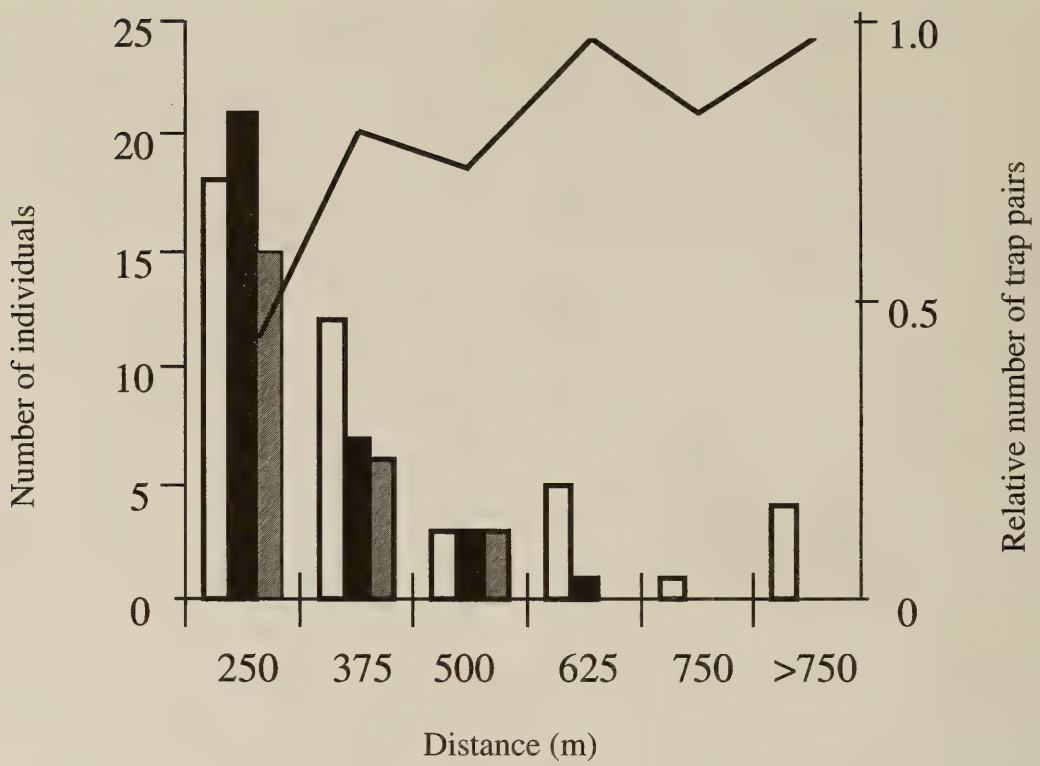

FIGURE 1. Distribution of distances moved by woodland rodents within large trapping grids in New Brunswick, Canada. White bars are *Peromyscus maniculatus*, solid bars are *Napaeozapus insignis*, and hatched bars are *Clethrionomys gapperi*. The relative number of pairs of traps within each distance class is indicated by the solid line.

long-distance movements by either *N. insignis* or *C. gapperi*, with the exception of homing studies. For example, Bovet (1980) recorded successful homing by Red-backed Voles from as far as 600 m.

Seasonal differences in captures between Woodland Jumping Mice and the other species were not surprising, as jumping mice are true hibernators whereas Red-backed Voles and Deer Mice are winter active (Whitaker and Wrigley 1972). Our data were consistent with patterns of increased movement in late summer by murids and in early summer by zapodids. These seasonal patterns should be interpreted carefully however, as the analysis included both movements made within a trapping season, and between seasons. Thus, we actually measured the number of captures made after long-distance movements per season, rather than the season when the movement was actually made (which was often unknown).

Two additional sources of error must be considered when interpreting these data. First, we have not corrected for the uneven distribution of trap pairs within different distance classes. The number of trap pairs varied with distance (Figure 1) and in fact, appeared to bias the distribution of distances toward longer movements: there were fewer trap pairs at the shortest distances. This was further confounded by a second bias: the density of traps varied throughout the study grids as a result both of geometry and the nested trapping design. Rather than make questionable corrections against these two biases, we present unmodified data and caution the reader against over interpretation. Even with the inherent problems, these data are of value because of the scarcity of information on small-mammal movements (e.g., Wegner and Merriam 1990; Kozakiewicz and Szacki 1995; Merriam 1995).

We expect that many of the movements which we have operationally-defined as "long-distance" were actually dispersal movements. Such movements likely have important, albeit poorly understood, effects on small-mammal populations. We are particularly interested in the relationship between dispersal and spatial population structure. For example, Deer Mouse, Red-backed Vole, and Woodland Jumping Mouse populations exhibit heterogeneity in abundance at distances of 133 - 350 m, on the same landscapes where the present movement data was collected (Bowman et al. 2000). The spatial extent of the heterogeneity is consistent with the distribution of dispersal distances. This supports speculation that dispersal distance in small mammals is related to a scale of population heterogeneity (e.g., Krohne and Burgin 1990).

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Abundance of Stream Invertebrates in Winter: Seasonal Changes and Effects of River Ice

Melanie D. Martin[1], Richard S. Brown[2], David R. Barton, and Geoff Power

Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada
[1]Robin Drive, Apartment 6, Elmire, Ontario N3B 1X1, Canada
[2]Battele, Pacific Northwest National Laboratory, Ecology Group, MSIN K6-85, 902 Battelle Boulevard, P.O Box 999, Richland, Washington 99352, USA

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The association between anchor ice and stream invertebrate density in the drift and on the substrate were studied in the Grand River, Ontario, over two winters. Under certain climatic and geomorphological conditions, anchor ice can form a thick blanket on the bottom of rivers and streams. There were almost thirty times more aquatic insects in the drift on mornings after anchor ice developed than when anchor ice did not occur. Both Diptera (mostly chironomids) and Trichoptera were more abundant in the drift when frazil slush was present. During both winters the total density of insects in the drift decreased as the seasons progressed, regardless of the presence or absence of anchor ice on the day of sampling. Within drift samples taken after anchor ice events this relationship was seen in the orders of Diptera and Trichoptera. There was also a decline in the total number of insects in the surface layer of substrate as the winter progressed, particularly in the families of Chironomidae and Simuliidae. Anchor ice and frazil slush appear to be significant factors in invertebrate dispersal and their role in the winter ecology of aquatic invertebrates deserves much more study.

Key Words: Frazil slush, anchor ice, aquatic invertebrate, fish, dispersal, drift, Ontario.

During fall and winter, stream invertebrates are exposed to much different conditions than during warmer seasons. Colder temperatures result in a lower metabolism, and ice formations can cause drastic changes to habitats. During cold weather, subsurface ice commonly forms in areas with moderate to high turbulence. In turbulent areas not covered with surface ice, water temperatures can drop below 0.0°C; this is known as supercooling (Tsang 1982). While the water is supercooled, small ice crystals (called frazil ice) form in the water column. When these ice crystals adhere to the substrate they form anchor ice. Anchor ice can form thick blankets on the bottoms of rivers and streams (Tsang 1982). When stream temperatures increase, or anchor ice becomes thick enough to become buoyant, it lifts off of the stream bottom, carrying with it pieces of substrate, macrophytes, and aquatic invertebrates. This ice, called frazil slush, then becomes incorporated into the flow of the river and transports invertebrates downstream.

Due to the lack of equipment specialized for winter sampling, and to harsh working conditions, few papers have been published on winter invertebrate drift and the effect of anchor ice on invertebrate transport. Some authors suggest that anchor ice has no permanent effect on the removal of invertebrates from the substrate (Brown et al. 1953; Benson 1955). During observations at the Pigeon River, Michigan, Benson (1955) concluded that the daily release of anchor ice from the stream bottom served as a mechanism for the downstream dispersal of bottom organisms, although, the overall depletion of benthic fauna as a result of this was negligible. Brown et al. (1953) viewed aquatic organisms floating alongside dense masses of slush in the West Gallatin River, Montana, thus supporting the hypothesis that anchor ice may temporarily increase the number of bottom organisms in the drift. Similar to Benson (1955) however, their results also showed no decrease in the overall abundance of bottom invertebrates during the winter months.

Other authors suggest that anchor ice, and the scouring that occurs as a result, not only frees aquatic invertebrates from the substrate into the water column but continuously changes the benthic composition of the stream bed over the winter months (Maciolek and Needham 1952; O'Donnell and Churchill 1954; Reimers 1957). Reimers (1957) stated that areas where anchor ice commonly occurred experienced a gradual depletion in benthic fauna due to repeated scouring of the streambed. During Reimers' study at Convict Creek, California, there was a considerably lower food intake by trout midway through the winter in these habitats, which suggests lower availability of food after repeated anchor ice events.

These contradictory results make it unclear whether the severity and frequency of anchor ice events throughout the winter can change the forage available to fish or progressively reduce the benthic population through repeated disturbance. When we observed that masses of frazil slush were transporting sediment and debris downstream, we began collecting samples of

the frazil slush for examination and followed up with a benthic survey. Our objective was to determine whether anchor ice events are associated with changes in the density of stream invertebrates in the drift and on the substrate. To achieve this goal, both drift and substrate samples were collected during periods when anchor ice occurred and when it was absent.

Study Area and Methods

The study was conducted along a 10 km reach of the Grand River (43°38'-43°4'N, 80°26'-80°2'W), Ontario in the Elora Gorge Conservation Area. The river channel in the study area has a relatively low gradient (mean 1.4 m km^{-1}) and flows in an open valley.

Invertebrates in the drift were collected during periods when anchor ice was present and when it was not present over two winters (21 January–20 March 1998 and 16 December 1998–23 February, 1999; Table 1). For drift samples with frazil slush, the amount of drift sampled (m^3) was determined by multiplying the amount of frazil slush collected (20–23 litres) by the estimated fraction of frazil in the drift and converting the units to cubic metres. The fraction of frazil slush in the drift was estimated by taking samples of the water column with a graduated cylinder and recording the ratio of frazil slush to water. Repeated samples were taken and the mean was used to estimate the fraction of frazil slush in the drift. The drift net (opening of 0.05 m^2, 2 mm mesh size) was deployed for a maximum of 3–5 minutes for each sample, depending on the amount of frazil slush in the drift. For drift samples without frazil slush, the amount of water sampled (m^3) was measured by multiplying the area of the net opening (0.09 m^2) by the water velocity ($m \cdot s^{-1}$) and the amount of time (s) that the net was in the flow. Dual drift nets, each with a net opening of 0.09 m^2 and mesh size of 180 micrometers collected drift for 30–60 minutes per sample. Drift samples were collected between 09:00 and 13:00. All samples were filtered through 180-micrometer mesh, then preserved in 85% ethanol. Samples with frazil slush were melted before being filtered. Organisms were counted and identified to family, when possible, using McCafferty (1981). Some organisms were missing appendages and/or were physically damaged to the point where identification to family was unreliable. In such cases, they were identified only to order.

Data from both winters (1997–1998 and 1998–1999) were used in comparing the number of organisms in drift samples with and without frazil slush. To determine if there was a difference in the number of insects in the drift when frazil slush was present and when not present, a Mann-Whitney U test was performed since data were not normal (determined with a Lilliefors test). Frazil slush samples collected in 1997–1998 were used to determine invertebrate density trends over the winter in the drift when frazil slush was present. Similarly, the drift samples collected in 1998–1999 were used in determining seasonal trends for drift without frazil slush. To determine these relationships, regression analysis was performed on the abundance of invertebrates per day in the drift when frazil slush was present and when frazil slush was not present. For the purposes of this analysis (and the analysis of invertebrates on the substrate), the earliest day on which samples were first collected in both years, 16 December, was used as the starting date of winter. Since not all relationships between invertebrate abundance and day of winter were linear, the type of regression analysis applied (linear or polynomial) was that which provided the most appropriate degree of fit.

Drift samples with frazil slush were collected in three different locations: at transect #1, 4.9 km downstream from transect #1 and 8.4 km downstream from transect #1. Drift samples without frazil slush were collected at transect #2 (0.6 km downstream from transect #1). There were no barriers to drift in the study area.

Fifty-two substrate (rock) samples (mean = 5 rocks per day) were collected between 16 December 1998 and 8 March 1999 (Table 1). Rocks (mean diameter = 8.68 cm; SD = 3.03) were selected in riffles along transect #1 and transect #2 (approximately 600 m apart) in the Grand River, Ontario. A small dip net (180-micrometer mesh) was used to trap invertebrates that had come loose off the rock when lifted out of the water. Each rock was put into a small container and rinsed with 85% ethanol. Insects on the net were rinsed into the container with 85% ethanol. All of the rock samples were scrubbed with a soft brush and handpicked with forceps to free the invertebrates from the rock surface. The sample was then filtered through the 180-micrometer screen and the material retained was stored in 85% ethanol until identified. The surface area of each rock was estimated by measuring the three largest diameters of the rock (Dall 1978). Both transects were marked so that rock samples and flow measurements could be taken at the same location on subsequent dates. Water velocities (mean and bottom) were measured using a Sigma Doppler flow meter.

At a 5 m^3 s^{-1} discharge rate (approximate winter base flow) transect one had a mean depth of 23 cm (N = 6, SD = 0.06) and mean velocity of 0.21 m s^{-1} (N = 6, SD = 0.11). Transect two had a mean depth of 24 cm (N = 7, SD = 0.10) and mean velocity of 0.68 m s^{-1} (N = 7, SD = 0.45). Substrate in both transects was predominantly large cobble. Since there were no significant differences ($p > 0.05$) between depths or water velocities (Mann-Whitney U test since data were non-normal), data for both transects were grouped. Regression analysis was used to determine if there was a trend in the overall insect abundance on the substrate over the winter. ANCO-

TABLE 1. The number of invertebrate samples taken from the drift and substrate when frazil ice was present or absent in the Grand River, Ontario.

Date	Number of samples		
	Drift with frazil ice	Drift without frazil ice	Substrate samples
21 January 1998	3	-	-
26 January 1998	2	-	-
6 February 1998	3	-	-
16 February 1998	2	-	-
11 March 1998	3	-	-
12 March 1998	4	-	-
13 March 1998	3	-	-
16 March 1998	3	-	-
17 March 1998	3	-	-
16 December 1998	-	1	6
18 December 1998	-	1	6
23 December 1998	-	3	3
31 December 1998	1	-	6
6 January 1999	-	1	3
13 January 1999	-	2	6
20 January 1999	-	2	6
3 February 1999	-	2	6
8 February 1999	-	2	6
21 February 1999	1	-	-
23 February 1999	4	-	5
8 March 1999	-	-	4

VA was used to determine if a consistent relationship existed between the day of the winter and abundance of aquatic invertebrates in both the drift (without frazil slush) and on the substrate.

To determine if the density of invertebrates in the drift was influenced by water discharge, water discharge on sample days when frazil slush was not present was compared to water discharge on days when frazil slush was present. This was done using a Mann-Whitney U test since data were not normal. Subsequently, regression analysis was used to determine if there was any relationship between water discharge and invertebrate density.

Results

Drift

There was a significantly ($p < 0.05$) larger number of drifting invertebrates on mornings after anchor ice events (mean 118.0 organisms/m^3 drift, SE = 18.6) than when anchor ice events did not occur (mean 4.2 organisms/m^3 drift, SE = 1.8). Both Diptera and Trichoptera were significantly ($p < 0.05$) more abundant when frazil slush was present, but there were no significant ($p > 0.05$) differences in densities of Ephemeroptera and Annelida. Within the order Diptera, there was a significantly ($p < 0.05$) larger number of chironomids in the drift when frazil slush was present (40.5/m^3) than when it was not present (1.8/m^3). There were no significant ($p > 0.05$) differences found in the drift within the families of the order Trichoptera. Nearly all of the Trichoptera in the drift samples were species of the family Hydropsychidae (90%) in 1999 and the family Lepidostomatidae (75%) in 1998. One factor that may have influenced these results is that river discharge was significantly ($p < 0.05$) higher on days when frazil slush was present (mean 9.5 m^{3}s^{-1}, SD = 7.3, range 1.5–28.0) than when frazil slush was not present (mean 2.4 m^{3}s^{-1}, SD = 1.5, range 1.6–5.0). However, no significant ($p>0.05$; $r^2 = 0.03$) relationship between water discharge and invertebrate density was found in samples when frazil slush was present.

Total changes over winter in drift

During the winters of 1997–1998 and 1998–1999 the density of animals in the drift decreased significantly ($p < 0.05$) as the seasons progressed, regardless of the presence or absence of frazil slush on each sampling day (Figure 1). In drift samples taken after anchor ice events (1997–1998 field season), both Diptera and Trichoptera (especially Lepidostomatidae) showed significant ($p < 0.05$) negative relationships between drift density and day of the winter. There was no significant ($p > 0.05$) trend in either Annelida (Class Oligochaeta) or Ephemeroptera. No significant ($p > 0.05$) relationships were found among individual taxonomic groups sampled when no anchor ice was present (1998–1999 field season).

Benthos

The total number of insects in the surface layer of substrate declined significantly ($p < 0.05$) as the winter progressed (Figure 2). There was a rebound in numbers following a period when surface ice covered most of the river and anchor ice did not form. Invertebrate densities decreased again when the surface ice cover was gone and nightly anchor ice formations again occurred.

When analyzed by order, only Diptera declined significantly ($p < 0.05$) over the winter (Figure 3). This significant ($p < 0.05$) negative trend was seen in the families Chironomidae and Simuliidae, when analyzed separately, but not in Empididae, Tipulidae, Athericidae or Ephydridae. The relationship between day of winter and insect abundance paralleled the same relationship found between day of winter and insect abundance in the drift (with frazil slush). There was however, no significant ($p > 0.05$) relationship between water temperature and abundance of aquatic invertebrates on the substrate over the winter.

Discussion

There are many variables in the natural riverine environment that influence aquatic invertebrate distribution from year to year. Natural disturbances such as summer flooding, winter freezing and spring thawing, moving ice, and rapidly fluctuating temper-

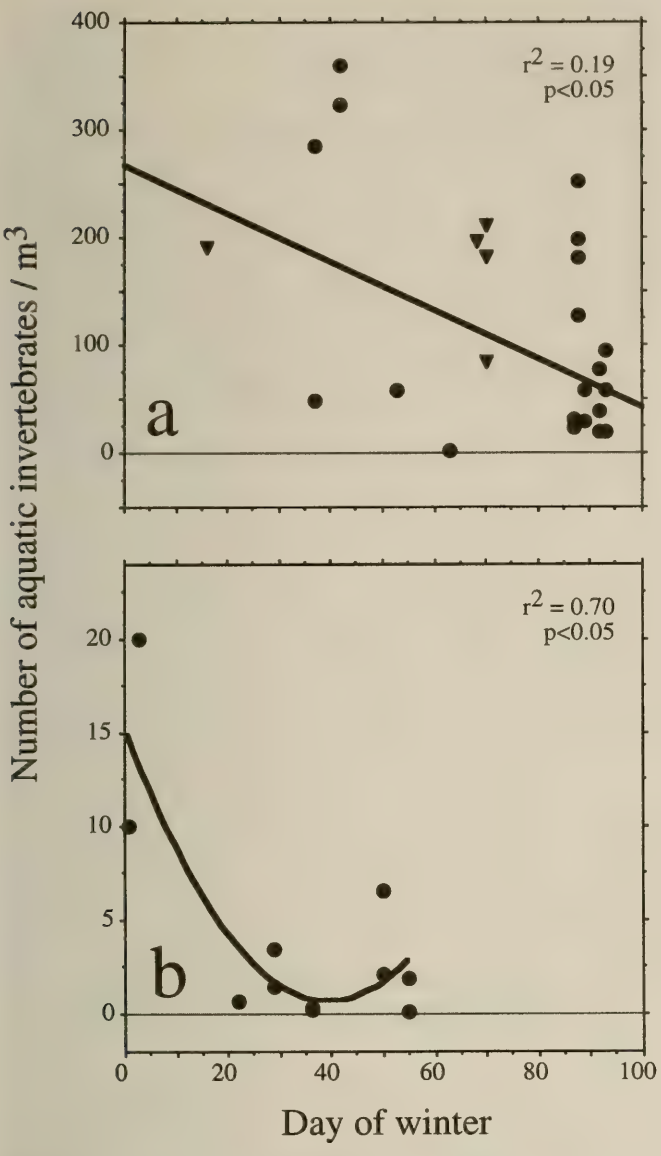

FIGURE 1. (a) Regression plot of the number of aquatic invertebrates collected in the drift on days when frazil ice was present from 21 January to 17 March 1998 and from 31 December 1998 to 23 February 1999 (shown as triangles) in the Grand River, Ontario. The regression analysis includes only data from the first winter. (b) Regression plot of the number of aquatic invertebrates collected in the drift on days when frazil slush was absent from 16 December, 1998 to 8 March 1999 in the Grand River, Ontario. 16 December was designated as Day 1 of the winter for both seasons. Note that the scale of the y axis varies between panels.

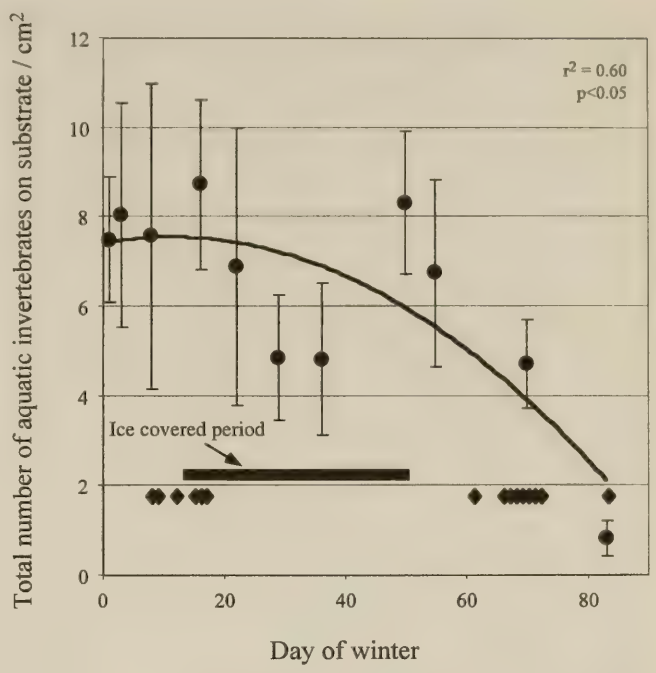

FIGURE 2. Regression plot of mean (± SD) number of aquatic invertebrates found on the substrate (organisms / cm^2) on different days from 16 December 1998 to 8 March 1999 in the Grand River, Ontario. Presence of frazil slush and anchor ice at the sampling site (diamonds) and presence of a surface ice cover (a solid line) in the pool upstream of the sampling site are also indicated.

atures play important roles in the distribution and survival of aquatic invertebrates (Miller and Stout 1989). Anchor ice and frazil slush were the main focus of this study and appear to be important factors in invertebrate dispersal. Since the greatest abundance of immature aquatic insects occurs during the winter season (Maciolek and Needham 1952; Reimers 1957), any conclusions about the dispersal or removal of aquatic invertebrates by anchor ice are important in understanding invertebrate and fish ecology.

Anchor Ice

The importance of anchor ice to benthic organisms is not due to low water temperatures (near 0.0°C) as many aquatic invertebrates are capable of surviving temporary freezing (Olsson 1981; Andrews and Rigler 1985) but due to its mechanical force on the substrate. As frazil ice crystals adhere to the substrate overnight or as the anchor ice releases, benthic organisms are at risk of physical damage and entrapment. Some studies have shown that invertebrates are able to survive entrapment in the ice with little or no mortality (Brown et al. 1953; Benson 1955). We also observed living invertebrates in the melted frazil slush samples. More importantly, our results show that sequential anchor ice events can change the local benthic population density. On days when anchor ice was released from the streambed, the density of invertebrates in the drift was much larger than when no anchor ice was released.

The frequency of frazil and anchor ice formations depend on climate. For these formations to occur, sub-freezing air temperatures are required but a solid surface ice cover must not be present. Freshwater ice cover in Canada is highly variable, from periodic skims in southerly temperature regions to mean thicknesses over 2 m on high-latitude rivers (Prowse

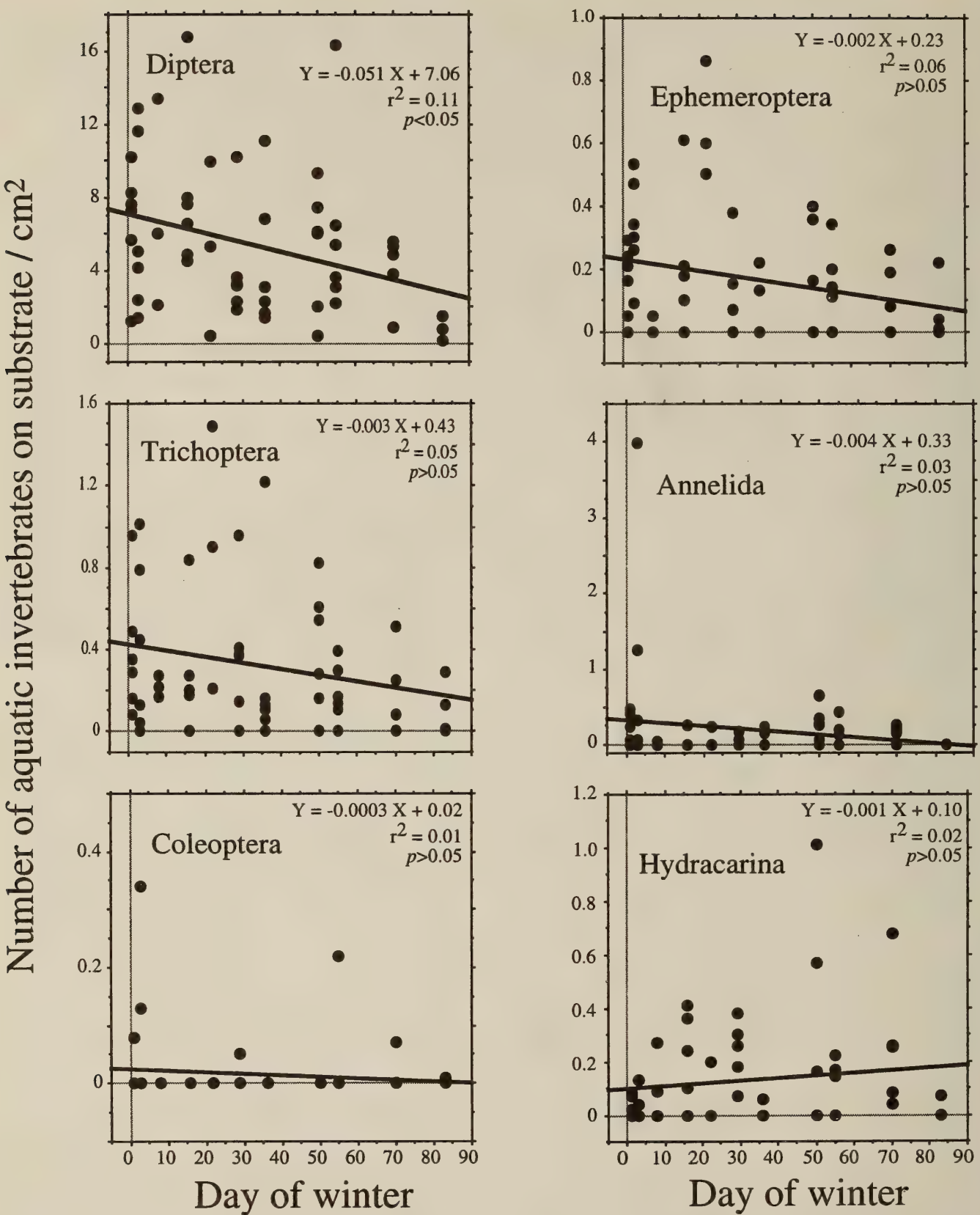

FIGURE 3. Regression plot of the number of aquatic invertebrates in six different orders found on the substrate (organisms / cm²) on different days from 16 December 1998 to 8 March 1999 in the Grand River, Ontario.

1990). Mean freeze-over dates, mean ice thickness, and mean ice-free dates are provided by Allen (1977) and reviewed by Prowse (1990). In many of the colder parts of Canada, streams have a short freeze-up period followed by a fairly stable period of surface ice cover until spring break-up (Prowse 1995). This occurs in the northern part of the country, and much of the prairie provinces (Beltaos 1997). In more moderate areas of Canada, such as the southern parts of Ontario, Quebec, and British

Columbia, and the Atlantic provinces, ice covers remain for a shorter period of time and both spring and mid-winter ice break-ups are common (Beltaos 1997). The Grand River is representative of the winter environments expected in moderate areas of Canada. Thus, frazil and anchor ice formations can occur frequently during the periods when a solid surface ice cover is not present. The conditions in the Grand River were favourable for anchor ice formation (water temperatures at or near 0.0°C and air temperatures below -5°C) on at least 42 nights during the winter of 1997–1998 and 57 nights during the winter of 1998–1999.

The increased insect abundance in the drift may temporarily elevate the amount of food available for fish. Reimers (1957) observed trout feeding aggressively among floating frazil slush, suggesting that the organisms were being transported downstream with the frazil slush. It should not be inferred, however, that this would increase the amount of forage available for fish because the organisms may be trapped in the floating frazil slush and not available for fish consumption.

Benthic composition

Most of the aquatic invertebrates found in our study area in the drift and on the substrate were Diptera, with Chironomidae, Tipulidae, and Simuliidae, respectively, being the most numerous families. These results agree with other winter findings in temperate streams and rivers (Clifford 1978; Colbo 1979; Mills et al. 1981), although some studies show Trichoptera as the most abundant order followed by Diptera (Brown et al. 1953; Benson 1955). In Newfoundland streams, Colbo (1979) observed that simuliid population density in a stream normally increases between December and April. However, in our study, the number of simulids on the substrate decreased as the winter progressed. Colbo (1950) also noted that certain Simuliidae larvae were absent or rare in zones where anchor ice occurs. This would compare favourably with our observations that the release of anchor ice removed larvae from the streambed and increased the number in the drift on days when frazil slush was present.

In comparison, densities of Chironomidae, (another common family of the order Diptera) may be highest in December and January, then gradually decrease until May (Clifford 1978). Conversely, our results show that the number of Chironomidae decreased in the substrate throughout December and January. Although Clifford (1978) suggests that population density trends can be attributed to various phenomena such as the appearance of new generations, delayed hatching, overlapping generations and available habitat, our observations indicate that this decrease in Chironomidae may be exacerbated by anchor ice. If so, this abrupt change in drifting density could be very important to fish species which prey on these invertebrates, particularly Chironomidae, which normally show a distinct periodic drifting pattern (McCafferty 1981). Further work to confirm these findings is advised, however, since a large amount of influence on the regression is due to the low invertebrate abundance on the substrate during the last winter sample.

This study provides evidence that anchor ice events correlate with changes in the local density of stream invertebrates and may play an important role in the dispersal of aquatic invertebrates in the Grand River. Our finding that invertebrates were more abundant in the drift when frazil slush was present than when it was absent suggests that the anchor ice removed invertebrates from the streambed causing them to be carried off by the drift. In addition, the number of stream invertebrates in the drift and on the stream bottom was gradually reduced over the winter. This effect may not occur in all rivers. Anchor ice forms in turbulent areas which are not readily covered by surface ice. If such areas are distributed along a river, invertebrates dislodged will resettle downstream and the overall effect on the stream benthos will be minimal. The largest impact from the removal of invertebrates may be areas directly below reservoirs, where invertebrates fall from the drift, preventing recolonization of areas which are depopulated by anchor ice. Warm water discharged from the dam precludes formation of anchor ice for a short distance downstream (depending on air temperatures) reducing the supply of replacement organisms. Depletion of the benthic fauna over the course of the winter may be a fairly widespread phenomenon as most rivers throughout the world have impoundments.

In future studies, it is recommended that invertebrate densities and distribution in the substrate be sampled prior to the formation and immediately after the release of anchor ice. This type of disturbance study (Underwood 1994) may provide more insight into the immediate influence of anchor ice.

Additionally, the restrictions of winter sampling make it difficult to control each of the variables that usually influence invertebrate density. Comparative sampling of neighbouring streams, one with anchor ice and one without anchor ice (possibly below a hydroelectric dam) which have similar structure, flow, temperature, etc., would be advantageous. One ecological condition that has not been considered during this research, but that may prove significant, is how feeding habits of fish change in association with anchor ice events or throughout the winter. Feeding habits of fish could be monitored and any analogous changes in benthic composition could be identified. During winter, aquatic invertebrates are clearly exposed to highly variable environments which may have large impacts on their population

densities. Thus this area of ecology deserves much more research.

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Establishment of a Breeding Population of Canada Geese in Southern Quebec†

JEAN-FRANÇOIS GIROUX[1], JOSÉE LEFEBVRE[1], LUC BÉLANGER[2], JEAN RODRIGUE[2] and STÉPHANE LAPOINTE[1]

[1]Université du Québec à Montréal, Département des Sciences biologiques, C.P. 8888, Succursale Centre-ville, Montréal, Québec H3C 3P8, Canada
[2]Canadian Wildlife Service, 1141, route de l'Église, C.P. 10 100, 9e étage, Ste-Foy, Québec G1V 4H5, Canada

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We documented the natural establishment of a breeding population of Canada Geese (*Branta canadensis*) on four islands located in the St. Lawrence River near Montreal. Number of nests increased from 3 in 1992 to 50 in 2000. We estimated that the population is currently growing at 36–46% per year. Over the years, nest success was high with 80% of the nests hatching at least one egg giving a Mayfield estimate of 66%. Morphometric measurements of geese nesting and molting in southern Quebec conform to those of Giant Canada Geese (*B. c. maxima*). Resightings of banded and neck-collared geese revealed that two birds marked in New York and one in Michigan, as part of resident flocks, have colonized the islands. Moreover, natal-fidelity of a female hatched on one of the islands indicates that the breeding population will continue growing. The colonization of the islands may result from the expansion of the resident populations of southern Ontario and eastern United States or from escapes from captive flocks. We also hypothesize that the establishment could be related to the use of the area by molt migrant resident geese that may return the following spring to breed. We recommend that management actions be taken to prevent establishment of a larger population of summer resident geese in southern Quebec. Otherwise, we predict that problems like those caused by resident Canada Geese established in urban and suburban settings elsewhere will occur. Climatic changes in a near future may also incite some Canada Geese to winter in southern Quebec and this could exacerbate potential problems.

Key Words: Canada Goose, *Branta canadensis*, population, control, breeding, molt migration, Quebec.

Recent establishment of breeding populations of Canada Geese in southern Canada and central and eastern United States have resulted from the release of captive birds or transplantation programs (Blandin and Heusmann 1974; Lumsden 1981; Hindman and Ferrigno 1990). These introductions have been very successful as demonstrated in southern Ontario where numbers of Giant Canada Geese (*B. c. maxima*) had reached 350 000 birds in fall 1998 (Dennis et al. *in press*). The same situation occurred in Europe (Madsen and Andersson 1990; Allan et al. 1995). Reasons for these introductions included a desire to restore an extirpated subspecies like in southern Ontario, to increase hunting opportunities and to add wildlife to adorn parks and country estates (Lumsden 1981; Madsen and Andersson 1990). As well, attempts to reduce local goose problems in one area have involved transplantation of Canada Geese to other areas (Hindman and Ferrigno 1990). Attractive feeding sites such as lawns in parks or golf courses, where the presence of small waterbodies and the lack of predators (including hunters whose activities are often limited in urban and suburban settings) are contributing to the establishment of breeding populations of Canada Geese (Conover and Chasko 1985; Conover and Kania 1991; Converse and Kennelly 1994). In the Atlantic Flyway, Canada Geese breeding south of 47° N of latitude are considered resident and consist mainly of Giant and Western Canada Geese (*B. c. moffitti*) (Hindman and Ferrigno 1990). Their population was estimated at 1.1 million birds in spring 1999 (Anonymous 1999*). Although referred to as residents, non-productive Giant Canada Geese (subadults, non- breeders and failed breeders) may migrate north to molt (Abraham et al. 1999; J. Rodrigue, unpublished data).

Recent increases in the number of resident Canada Geese have given rise to nuisance problems in many areas. Geese foul beaches, parks and golf courses with droppings, overgraze lawns, cause agriculture damage and constitute aircraft hazards (Blokpoel 1976; Conover 1985; Conover and Chasko 1985; Hindman and Ferrigno 1990; Allan et al. 1995; Ankney 1996; Anonymous 1999*). Human pathogens have also been isolated in Canada Goose feces (Graczyk et al. 1998). Although the contamination by these pathogens is not easily diagnosed, the risk of infection is probably low (Anonymous

†Ideas and recommendations presented in this paper reflect the personal point of view of the authors and do not represent the position of the Canadian Wildlife Service of Environment Canada.
*See Documents Cited section.

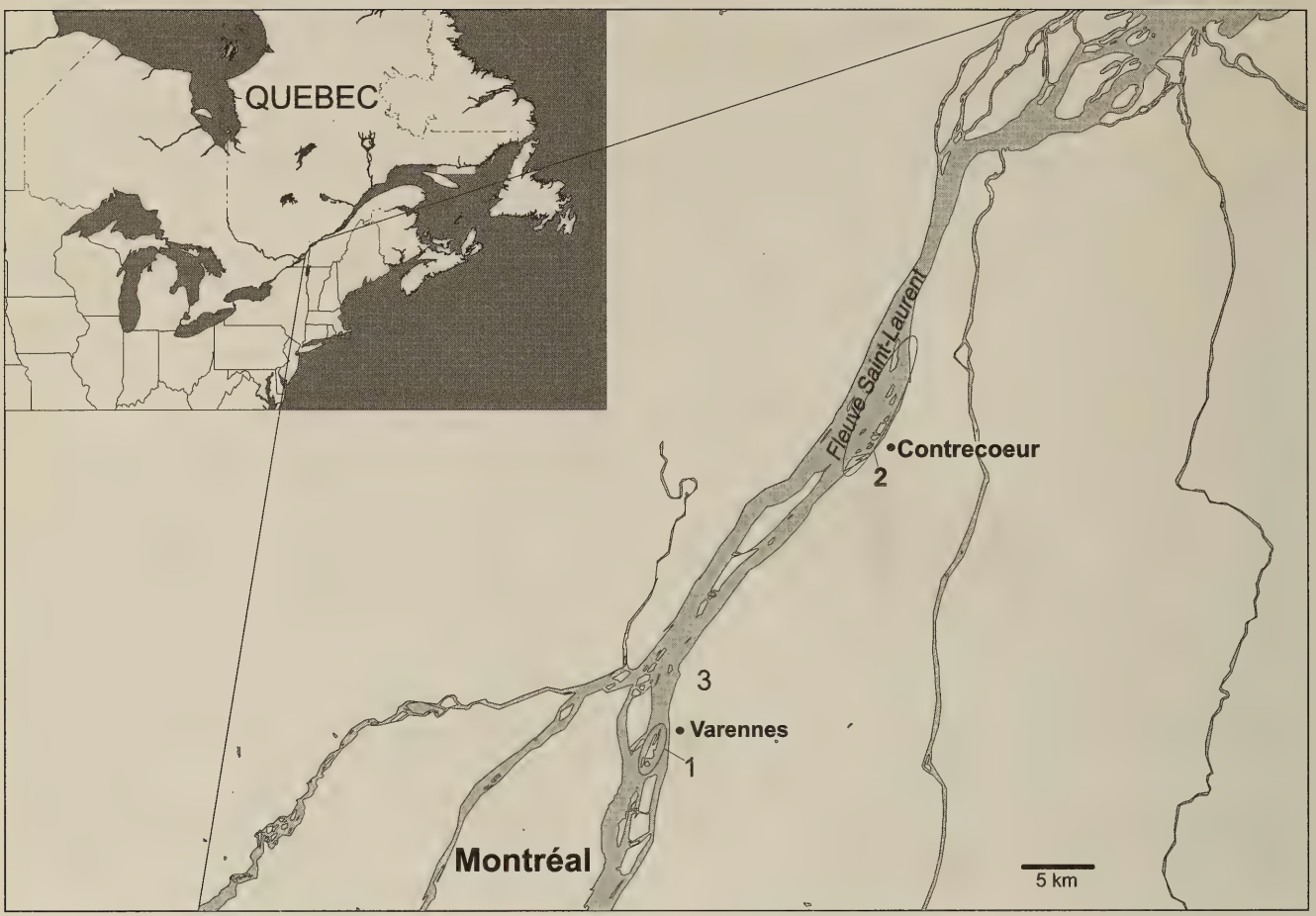

FIGURE 1. Map showing location of the four Varennes islands (1), Les Îles de Contrecoeur National Wildlife Area (2) and the Dow Chemical plant at Varennes (3), Quebec.

1999*). There is also some concern that competition for food between molt-migrant Giant Canada Geese and the migratory sub-species (*B. c. interior* and *B. c. canadensis*) on the northern breeding grounds could affect the reproductive output of migratory populations (Ankney 1996; Abraham et al. 1999). Finally, genetic integrity of the different stocks could be threatened by pairing of resident and migratory geese (Wendt and Boyd 1990).

Little is known about the natural establishment of Canada Geese outside their traditional breeding range. In this paper, we document establishment of a breeding flock of Canada Geese near Montreal in southern Quebec. It is unlikely that pre-settlement characteristics of southern Quebec resemble the prairie-like conditions characterizing Giant Canada Geese breeding habitat (Hanson 1965). We also report the origin and morphometric data of a sample of birds and characterize the molt migration of resident Canada Geese to Quebec. We finally propose possible mechanisms by which this establishment occurred, discuss potential consequences, and suggest management strategies.

Study Area and Methods

We conducted our study on four islands near Varennes (45°40′ N, 73°27′ W) located within the St. Lawrence River, 15 km northeast of Montreal (Figure 1). The four islands included Grande île (57.4 ha), Masta (9.4 ha), St-Patrice (16.6 ha) and Île-aux-Fermiers (28.1 ha) for a total of 111.5 ha. About 100 cows are pastured on the islands between June and November each year (Lapointe et al. 2000). A rotational grazing system was established in 1992: some pastures (36.8 ha) were improved by seeding Timothy (*Phleum pratense*), Yellow Sweet-clover (*Melilotus officinalis*), Brome (*Bromus inermis*) and clover (*Trifolium* spp.). Other portions of the islands were converted as dense nesting cover (DNC) for ducks (20 ha) by seeding Reed Canary Grass (*Phalaris arundinacea*), Western Wheatgrass (*Agropyron smithii*) and Crested Wheatgrass (*Agropyron cristatum*). Finally, some portions were left as idle fields with no cows (39.1 ha) or as unimproved pastures (15.6 ha), both dominated by Tufted Vetch (*Vicia cracca*), Redtop (*Agrostis alba*), Red Fescue (*Festuca rubra*) and Kentucky Bluegrass (*Poa pratensis*). No trees or shrubs are found on the islands as a result of recurrent grazing by cattle. There are two inland marshes (<5 ha) that are permanent and a few temporary ponds that become dry in summer. Emergent vegetation in marshes consists

primarily of Narrow-leaved Cattails (*Typha angustifolia*) and scattered clumps of Giant Bur-reed (*Sparganium eurycarpum*) and arrowhead (*Sagittaria* spp.). More details about the study area and the management practices are given by Lapointe et al. (2000).

All portions of the islands were visited during the breeding period every 10–15 days in 1992–1994 and 1999–2000 and every 3–5 days in 1996–1998. No nest search was conducted in 1995. A nest was defined as a bowl with one or more eggs or with fresh down. Each nest was marked at 5 m with a plastic pole and located on aerial photos (1:10 000). The presence of the female, the number of eggs and their incubation stage, determined by flotation (Walter and Rusch 1997), were noted when the nest was first located. During our regular visits to the islands, each nest was inspected when the pair was absent or after the expected hatching date. A nest was considered successful if at least one egg hatched. The identity and origin of some birds nesting on the islands was established by approaching the nest and using a spotting scope and either reading the code on neck collars (Hestbeck 1995) or the number on the USFWS aluminum bands.

In July 1999, flightless geese were captured by driving them toward a funnel-shaped trap on the Varennes islands and at a nearby molting area on the already fenced grounds of the Dow Chemical plant at Varennes (Figure 1). The birds were aged (adult and juvenile), sexed by cloacal examination and leg banded. Morphometric measurements taken by the same observer (JR) included skull, culmen and total tarsus length (Dzubin and Cooch 1992). We used unpublished discriminant functions developed by T. J. Moser (US Fish and Wildlife Service, personal communication) for differentiating Canada Geese of the Atlantic Population that breed between Ungava Bay and the east coast of Hudson Bay from resident Canada Geese of the Atlantic Flyway. The equations for males and females were Y = -87.961 + 0.463 culmen +0.499 skull and Y = -86.328 + 0.581 culmen +0.476 skull, respectively. Values greater than 0 for Y represent resident *B. c. maxima*.

The chronology of molt migration of 1130 Canada Geese in southern Quebec was established in the summer of 1991 at Les Îles de Contrecoeur National Wildlife Area, 25 km downstream from Varennes (Figure 1). Each day, five observers recorded the number of geese flying over the area or staging on water.

Results

We found 136 nests during our study: 3 in 1992, 4 in 1993, 5 in 1994, 10 in 1996, 17 in 1997, 21 in 1998, 26 in 1999 and 50 in 2000. Using the exponential model $N_t = N_0 e^{rt}$, we estimated a growth rate ($\lambda = e^r$) of 1.41 with a 95% CI of 1.36–1.46 ($R^2 = 0.99$; $F_{1,7} = 498$; $P < 0.0001$).

Over the years, Canada Geese initiated nests between 25 March and 17 May with 70% of them between 10 and 25 April. Clutch size averaged 5.5 ± 0.14 (SE) with a mode and median of 6 eggs (n = 125). Apparent success of 129 nests with known fate was 80% with a Mayfield nest success of 66%. Desertion and predation occurred at 5 and 12 nests, respectively. All preyed-upon nests were emptied with no apparent sign of predators, although one Red Fox (*Vulpes vulpes*) was observed on the islands in 1999. Human disturbance, including egg removal, may have caused some predation and desertion. Three nests were flooded in 2000 during an unusual rise of the St. Lawrence River water levels in early May. Finally, infertile eggs had been laid in six nests that were abandoned after the normal incubation period.

Since 1996, 64 (53%) nests were established in the idle portions of the islands, 29 (24%) in dense nesting cover, 13 (11%) in unimproved pastures and 15 (12%) in improved pastures. Number of nests in the four habitats differed from expected based on the area covered by each habitat ($\chi^2 = 29.898$; df = 3; $P < 0.01$). There were proportionally more nests in idle fields and less in improved pastures.

Nine previously-marked birds were identified at Varennes. Two birds had been banded in July as adults (After Hatching Year) when molting at Wilson Hill Wildlife Management Area near Massena, New York, with resident geese. One of these birds banded in 1991 nested at Varennes every year of our study since 1994. One female, hatched on or near the Varennes Islands and banded as a local bird in 1993, nested successfully in 1997 and 1998. Another female that also nested for four consecutive years (1997–2000) was banded in winter 1995 as an adult near Albany, New York, where both resident

TABLE 1. Mean morphological measurements (mm) of Canada Geese captured in July 1999 in southern Quebec.

	Culmen		Total tarsus		Skull	
Sex	*x*	SE	*x*	SE	*x*	SE
Male (*n* = 41)	60.3	0.47	115.3	0.71	131.7	0.69
Female (*n* = 41)	57.3	0.37	108.5	0.60	124.4	0.49

and migrant geese winter. This goose was later observed in February 1996 at Long Island, New York (J. Hestbeck, Massachusetts Cooperative Fish and Wildlife Research Unit, personal communication). A female that initiated a nest during two successive years had been banded as a local in 1992 in a flock of resident Giant Canada Geese at Lower Brace Lake near Marshall, Michigan (G. Belyea, Michigan Department of Natural Resources, personal communication). Finally, four geese (2 males and 2 females) banded in July 1999 at Varennes were observed breeding on the islands in 2000.

In 1991, more than 95% of molt-migrant geese were recorded during the first three weeks of June. This pattern was subsequently observed each year in the Contrecoeur/Varennes area (J.-F. Giroux and J. Lefebvre, unpublished data). Moreover, since about 1995, about 50–200 geese spent part of the summer and early fall only 8 km from the Varennes islands (N. Rouette, Dow Chemical Canada Inc., personal communication). These birds molt within the fenced grounds of the Dow Chemical plant surrounded by a lawn with a pond.

There were no differences in any of the three measurements between adult birds captured in 1999 on the nesting islands and those at the nearby molting area ($P > 0.05$). The mean measurements obtained on these birds (Table 1) conform to the measurements given for *B. c. maxima* for the Atlantic Flyway resident population (T. J. Moser, personal communication) and for resident birds from southern Ontario (Merendino et al. 1994). Using discriminant functions developed by T. J. Moser, only two birds (2.4%) did not fit the measurements of Giant Canada Geese. These were two males, both conforming to Atlantic Population migrant birds. The three previously-banded birds that nested on the Varennes islands in 1999 were captured and identified as *B. c. maxima*.

Discussion

There are approximately 275 islands in the St. Lawrence River and in its tributaries near Montreal (Figure 1). Canada Geese became established on other islands near Varennes because 11 nests were found during sporadic visits there since 1992 (L. Bélanger and J. Lefebvre, unpublished data). Moreover two broods were observed in 1999 at Les Îles de Contrecoeur National Wildlife Area (Figure 1; J. Lefebvre, unpublished data). Three Canada Goose nests were also initiated in 1998 and 1999 on the grounds of the Dow Chemical plant (N. Rouette, personal communication). The breeding population of resident Canada Geese in the St. Lawrence River lowlands of southern Quebec (approximately 30 540 km^2 excluding the river itself) was estimated at 710 ± 162 indicated breeding pairs during helicopter surveys conducted in 1998–1999 (D. Bordage, Canadian Wildlife Service, personal communication). In addition, 195 pairs were estimated on the islands and the shore of the St. Lawrence River (approximately 1300 km^2 between Cornwall and Matane) in 1990–1992 (D. Bordage, personal communication). This gives a minimum estimate of 900 pairs for southern Quebec.

The carrying capacity of southern Quebec for Canada Geese is unknown, but many safe nesting islands and farm ponds, availability of feeding sites and limited hunting opportunities, in suburban settings, are ideal conditions for growth of a breeding population of resident Canada Geese (Conover and Chasko 1985; Conover and Kania 1991; Converse and Kennelly 1994). The 36–46% annual growth rate observed on the Varennes islands may not be representative for the entire southern Quebec population because islands are attractive nesting sites for Canada Geese. Nevertheless, high natality resulting from large clutch size and high nesting success, faithfulness of females to the nesting islands, and natal-site fidelity will undoubtedly contribute to population expansion (Allan et al. 1995). Based on Ettl's (1993) data for 15 urban goose populations, which showed a good fit ($R^2 > 0.5$) to an exponential growth function, we calculated an average annual growth rate (λ) of $18 \pm 2\%$ which means that these populations double every 5–6 years. Ankney (1996) reported that the resident population of Canada Geese in southern Ontario also doubles every five years. The Canada Goose population of southern Quebec is increasing at a comparable or even greater rate. Given an 18% growth rate, the population would reach > 20 000 breeding pairs in 20 years.

The observation of two nesting birds that had been banded in New York, 140 km from Varennes, and one from Michigan, indicates that the significant increase in numbers of resident geese in southern Ontario and eastern United States could have lead to the extension of breeding populations into southern Quebec. Birds escaped from captive flocks are also a potential source for establishment of breeding flocks. There are about 300 permit holders of captive birds in Quebec who reported owning nearly 3000 Canada Geese in 1995 (G. Gagnon, Environment Canada, personal communication).

Most migratory Canada Geese have left southern Quebec by mid-May (Cazelais 1992; Chabot and St-Hilaire 1996*). Therefore, birds passing through the area during the first weeks of June are molt migrants (Abraham et al. 1999). Measurements of geese nesting and molting at Varennes confirm that all but a few belong to *B. c. maxima*. Giant Canada Geese that previously came or passed through southern Quebec during their molt migration may have returned there to found the newly established breeding population. This hypothesis, however, needs to be confirmed by the marking of molt migrant geese in Quebec.

Band recoveries and recaptures of birds, banded during summer in southern Ontario and northeastern United States, confirm the presence of molt migrants along the Saguenay River near St. Fulgence (48°27′ N, 70°54′ W) and in northern Quebec between 52 and 62° N (J. Rodrigue, unpublished data; Hughes and Reed 1999*). If our hypothesis on the establishment of breeding populations by molt migrants is valid, colonization by breeding Giant Canada Geese of these more northern areas could be possible. The so-called resident Canada Geese may then become fully migratory and could jeopardize genetic integrity of migrant flocks of *B. c. interior* and *B. c. canadensis* (Wendt and Boyd 1990).

The increase in breeding Canada Geese in southern Quebec will likely augment the number of molt migrants to northern Quebec. Competition for food with migratory Canada Geese, especially during the brood-rearing period, could affect reproductive output of *B. c. interior* and *B. c. canadensis* (Ankney 1996; Abraham et al. 1999).

Many islands of the St. Lawrence River are used for cattle grazing (Bélanger and Lehoux 1995). On the Varennes Islands, however, cattle do not affect Canada Geese because most of the nests have hatched before cows are brought to the islands in late May/early June. Restricting cattle to portions of the islands results in idle fields that seem favored by Canada Geese. Lapointe et al. (2000) found more residual cover (dead vegetation) in idle fields and DNC than in other treatments. On the other hand, idle fields had less standing (live) vegetation than DNC, which would provide better visibility for nesting geese. Abandonment of these management practices to decrease the attractiveness of the islands for geese would not be justified considering that their benefits for nesting ducks (Lapointe et al. 2000) and songbirds (Lavallée 1998) far outweigh the current problems caused by Canada Geese.

Although most Canada Geese are not able to winter in southern Quebec because of the rigorous climate, the situation might change in the future with global warming. Nevertheless, we anticipate that the population expansion will cause problems such as those seen in eastern and central United States and southern Ontario (Conover 1985; Conover and Chasko 1985; Hindman and Ferrigno 1990; Ettl 1993; Ankney 1996). Golf courses, parks, beaches and agricultural areas are found all along the St. Lawrence River in southern Quebec. Only a few complaints about nuisance resident Canada Geese have so far been filed but the number increased in 1999 (G. Paquin, Environment Canada, personal communication). Waiting to manage local populations until numbers reach nuisance levels is not desirable (Ettl 1993). Reactive management plans are less likely to be cost-effective and politically acceptable than are preventive ones. We therefore recommend that management measures be taken to prevent further expansion of the population to avoid problems often associated with resident Canada Geese. This supports the recommendations of the Atlantic Flyway Council for Québec (Anonymous 1999*).

Further surveys should be conducted to locate precisely concentrations of birds and to follow the demographic evolution of the resident Canada Geese. This will help to identify areas where interventions should be directed. Consultation should be initiated with local stakeholders such as hunters, bird watchers, conservationists and municipal representatives to discuss population objectives and management strategies.

Several methods have been developed to restrain population growth such as relocation, harassment, egg spraying, male sterilization and scaring with dogs (Conover and Chasko 1985; Aguilera et al. 1991; Converse and Kennelly 1994; Christens et al. 1995; Smith et al. 1999; Castelli and Sleggs 2000). Simulation models, however, have revealed that harvesting a large proportion of geese every year (e.g. culling molting birds) is the most efficient technique to reduce numbers of nuisance Canada Geese (Ettl 1993). This method does not usually receive general approbation by the public and less so by animal rights groups, but public opinion may be changing (Loker et al. 1999).

For southern Quebec, we first suggest liberalizing the current early hunting season (6–24 September) restricted to Canada Geese in agricultural lands. Increasing bag limits and season length and allowing hunting in more areas should maximize harvest of molt migrants and resident breeding birds while a judicious timing of this season should minimize mortality of the Atlantic Flyway population of migrants. This approach, however, will remain limited within urban and suburban areas for public safety reasons.

A second suggestion is to prevent Canada Geese from breeding successfully by spraying eggs with mineral oil or addling eggs. Nest sites can be easily located in spring because males often remain close to incubating females. Preventing hatching may be more politically acceptable than direct control of the birds. It might also be cost-effective for the St. Lawrence River islands because the population is still at a manageable level. However, considering that 80% of indicated breeding pairs are located elsewhere, the effectiveness of reducing the breeding success of geese on islands may be limited, and we may require a more extensive and expensive control program.

In conclusion, there is not a single strategy that will be totally effective in controlling the number of geese that will be economically feasible and acceptable by the majority of stakeholders. Reducing

reproductive output of the summer resident population of Canada Geese coupled with a more liberal early hunting season on both molt migrants and residents may maintain numbers at an acceptable level and minimize nuisance problems on public and private property. If these strategies fail, other alternatives including direct control of molt migrants and breeding residents (ex. food shelf programs) would have to be considered.

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Edge-related Nest Predation Associated With the Retention of Residual Trees in Harvested Hardwood Stands

RICHARD H. YAHNER[1], AMANDA D. RODEWALD[2], and SUSAN C. TALBOTT[2,3]

[1]School of Forest Resources and Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, Pennsylvania 16802, USA

[2]Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, Pennsylvania 16802, USA

[3]Present address: Eastern Neck National Wildlife Refuge, 1730 Eastern Neck Road, Rock Hall, Maryland 21661, USA

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We examined edge-related predation in June–August 1998 on artificial ground nests associated with the retention of residual trees in harvested oak (*Quercus* spp.)-hickory (*Carya* spp.) stands in a state in Pennsylvania. We tested the hypothesis that predation rates on nests did not vary with distance from edge in retention stands and adjacent unharvested forest stands. Artificial nests were placed during five time periods (trials) in three representative retention stands in Rothrock State Forest along random transects at four distances perpendicular to the edge: 50 m into the retention stand, at the edge, 50 m into the adjacent forest, and 150 m into the adjacent forest. Artificial nests consisted of three large brown chicken (*Gallus gallus*) eggs to simulate nests of Ruffed Grouse (*Bonasa umbellus*) and Wild Turkey (*Meleagris gallopavo*). Twenty-three % (82/358) of the nests were disturbed during the five trials combined. Nest fate was not influenced by the distance of nests from the edge ($P = 0.88$). We also found an interaction between trial and site ($P = 0.01$); in particular, one site (Cooper's Gap) had much higher predation rates during trials 3–5 when abundances of American Crows (*Corvus brachyrhynchos*) were higher at the site. Predation rates observed in our study were comparable to those found elsewhere in other harvested forests of Pennsylvania, where the abundance of crows is known to be relatively low. Nest predation rates in retention stands probably did not vary with distance from edge because nests were well concealed by a dense layer of ground-level vegetation regardless of distance from an edge. We hypothesize that variation in predation rates among sites may be explained by differences in the degree of heterogeneity, i.e., extent of edges and amount of habitat contrast, within and among adjoining habitats. We conclude that habitat conditions created by retention stands do not have a major negative effect on the nesting success of common, ground-nesting gallinaceous birds.

Key Words: artificial nest, bird, clearcutting, edge, even-aged management, forest, landscape, Pennsylvania, predation, retention stands.

Edge-related nest predation in fragmented landscapes has been well studied (see review by Paton 1994). Predation rates in forested tracts surrounded by agricultural landscapes are generally higher on nests located near edges compared to those nests located farther from edges; however, relationships between nest predation rates and distance from edge are much less likely to occur in managed forested landscapes, perhaps because of differences in predator communities between these two landscapes (Andrén 1995; Donovan et al. 1997; Hartley and Hunter 1998; Yahner 2000; but see King et al. 1998). Some studies in forested landscapes have shown that incidences of nest predation are associated with the degree of heterogeneity; i.e., extent of edges or amount of habitat contrast, within and among adjoining habitats in the local landscape rather than distance from edge (Yahner and Scott 1988; Yahner et al. 1989; Sargent et al. 1998).

Harvesting practices, such as clearcutting, not only create edge but also markedly change vegetative structure compared to unharvested adjacent habitat in the local landscape (e.g., Yahner 2000). Complete removal of overstory trees via clearcutting, however, has become a controversial practice for ecological and aesthetic reasons in much of the eastern deciduous forest (e.g., King et al. 1998; Yahner 2000). Harvesting practices, which retain individual trees, snags and small patches of trees within stands (termed variable-retention systems) are increasingly used across North America in an effort to meet forestry and ecological objectives (Franklin et al. 1997).

In 1992, the Pennsylvania Bureau of Forestry initiated a new practice to replace clearcutting on state forests, which is termed "even-aged reproduction with reservation guidelines" (hereafter termed retention stands, Boardman and Yahner 1999; Rodewald and Yahner 2000). This new practice permanently retains relatively high densities of live trees and snages in multiple crown and size classes of both commercially and non-commercially important tree species. In addition, the retention of trees produces gradual rather than abrupt edges (after Suarez et al. 1997) at the interface of the cut and the adjacent unharvested forest (R. H. Yahner, personal observation). Hence, state forests in Pennsylvania provide an excellent opportunity to examine how the retention of residual trees affects nesting birds.

Because the extent of state forest land in Pennsylvania is substantial (850 000 ha) and represents some of the largest remaining forested tracts in the eastern United States, an examination of edge-related nesting success in retention stands is needed. Furthermore, given the projected wide application of variable-retention systems in North America (Franklin et al. 1997), and understanding of their edge-related effects is important for avian conservation efforts. In our study, we tested the hypothesis that predation rates on artificial nests simulating those of common ground-nesting species of gallinaceous birds did not vary with distance from edge in retention stands in harvested forested landscapes of Pennsylvania.

Study Area and Methods

Our study was conducted in harvested oak-hickory stands in Rothrock State Forest, Huntingdon County, Pennsylvania. This state forest is located in the Valley and Ridge Province, which contains forest stands from 70–90 years old (Brooks and Birch 1988). Principal overstory trees are Northern Red Oak (*Quercus rubra*), White Oak (*Q. alba*), Chestnut Oak (*Q. prinus*), hickories (*Carya* spp.), Red Maple (*Acer rubrum*), Black Cherry (*Prunus serotina*), and Black Gum (*Nyssa sylvatica*) (Rodewald and Yahner 2000).

Retention stands have been established in Rothrock State Forest in lieu of clearcutting since 1992 (Boardman and Yahner 1999; Rodewald and Yahner 2000; Yahner 2000). This practice has the following guidelines: (1) retain an average basal area of at least 23–46 m^2/ha over the entire treatment area and > 12 trees/ha in the dominant, codominant, and/or intermediate class; (2) retain tree species representative of the pre-harvest stand; (3) retain all crown classes; (4) maintain natural spacing and consider leaving small groups of residual trees; and (5) select residual trees based on structural and species diversity.

We chose three retention stands that were representative of those created by the Bureau of Forestry in terms of size, shape, and age (Boardman and Yahner 1999; Rodewald and Yahner 2000). Turkey Hill and Cooper's Gap stands were 38 ha each, and the Spruce Mountain stand was 28 ha; each stand was oblong in shape, was typically about 300 m wide and at least 900 m long, and followed the contour of the adjacent ridge. Turkey Hill, Cooper's Gap, and Spruce Mountain were cut in 1993, 1994, and 1995, respectively. Stands were 2 to 15 km from each other, and amount of forest cover within 1.0 km of each cut ranged from 80 to 82% (A. D. Rodewald and R. H. Yahner, unpublished data). The remaining cover types within this 1.0-km radius consisted of early-successional and young forest, unimproved access roads, and scattered rustic cabins. There was no agricultural lands (cropland or pasture) were within the 1-km radius; distance of retention stands from agricultural lands varied from 1.9 to 3.1 km.

We selected three random transects per retention stand for nest placement during each trial; distances between adjacent transects were at least 100 m. These transects were selected from random points located at 100-m intervals along the boundary of each retention stand; a different transect was selected for each trial. Transects were oriented perpendicular to the retention stand-unharvested forest interface. Each transect extended 50 m into the center of retention stands but only 150 m into the adjacent forest because elevation, vegetation, and microclimate changed dramatically near the ridgeline in this area (Yahner and Smith 1990). Dense herbaceous vegetation (69–87% coverage; S. C. Talbott and R. H. Yahner, unpublished data) near ground level at the retention stand-adjacent forest interface and tree retention produced a gradual edge at the interface. Thus, we determined the exact location of the edge for placement of transects on the basis of paint markings remaining on large trees, which had served to delineate the boundary of the retention stand prior to its selective harvest.

We placed artificial ground nests during five time periods (trials) from early June through early August 1998 (Yahner and Wright 1985; Yahner and Mahan 1996a). Artificial ground nests consisted of three fresh, brown Domestic Chicken (*Gallus gallus*) eggs placed in a shallow depression near a tree, log, stump, or rock (e.g., Yahner and Wright 1985; Yahner and Mahan 1996a). We wore rubber-soled boots and latex gloves to minimize human scent when placing nests (Nol and Brooks 1982). Large brown chicken eggs (light brown to buffy in color, 52 × 40 mm) were used to simulate nests of Ruffed Grouse (*Bonasa umbellus*; buffy, 39 × 30 mm) and Wild Turkey (*Meleagris gallopavo*; pale buff or buffy white, 63 × 45 mm) (Harrison 1975; Yahner and Mahan 1996b). Ruffed Grouse and Wild Turkey are common, ground-nesting gallinaceous species within and near retention stands in Rothrock State Forest (Boardman and Yahner 1999).

Trial length followed those of previous nest studies using artificial ground nests (e.g., Yahner and Wright 1985; Yahner and Mahan 1996a), with a nest exposure of 6 days and 8 days elapsing between trials. During each trial, a nest was placed 15 m to each side of a transect at four distances from the edge: 50 m into the retention stand, at the edge, 50 into the adjacent forest, and 150 m into the adjacent forest. This experimental design gave 24 nests/stand in each of the five trials (n = 358 total nests; 2 nests were not relocated in trial 2).

We determined the fate (undisturbed, disturbed by avian predators, or disturbed by an unknown predator) after each trial. A disturbed nest had at least one broken or missing eggs. Nest appearance and mode of disturbance were used to classify predator type, e.g., peck holes suggested an avian predator (Rearden 1951; Yahner and Scott 1988; Hernandez et al.

1997), and other types of marks were attributed to unknown predators. Eggs and eggshell fragments were removed at the end of a trial. The relative abundance of potential avian nest predators, i.e., American Crows (*Corvus brachyrhynchos*) and Blue Jays (*Cyanocitta cristata*), were noted within 200 m of artificial nests at the time of placement and removal (Yahner and Scott 1988); time spent at a visit to a nest was about 5 minutes. A variety of other potential nest predators occurred in vicinity of the stands, e.g., included snakes, squirrels (*Sciurus* spp.), Eastern Chipmunks (*Tamias striatus*), Common Raccoons (*Procyon lotor*), Striped Skunks (*Mephitis mephitis*), and Black Bears (*Ursus americanus*) (R. H. Yahner, personal observation).

We examined the dependency of nest fate (undisturbed or disturbed) on distance from an edge (50 m into retention stand, edge [0 m], 50 m into adjacent forest, or 150 m into adjacent forest), trial (1–5), and site (Turkey Hill, Cooper's Gap, or Spruce Mountain) using a four-way test-of-independence (Dixon 1990). Likelihood ratios (G^2) were used to examine interactions between nest fate and the other three variables based on log-linear models (Sokal and Rohlf 1995).

Results

Twenty-three % (82/358) of the artificial ground nests were disturbed during the five trials combined (Table 1). Only 7% (6/82) of the disturbed nests had evidence of avian predation, based on the presence of peck holes in eggs. Disturbance rates by American Crows, however, may have been underestimated because crows are capable of carrying eggs away from an artificial nest (Montevecchi 1976); for instance, 50% (41/82) of the disturbed nests had at least one missing eggs, many of which may have been removed by crows. The relative abundance of American Crows ranged from 0.0/visit at Turkey Hill and 0.1/visit at Spruce Mountain to 1.7/visit at Cooper's Gap, whereas the relative abundance of Blue Jays was 3.7/visit at Turkey Hill, 1.1/visit at Spruce Mountain, and 0.2/visit at Cooper's Gap.

Nest fate was not dependent on the distance of nests from an edge ($G = 0.7$, df = 3, $P = 0.88$); disturbance rates ranged from 20% at nests 150 m into the adjacent forest to 24% at nests at both the edge and 50 m into the forest (Table 1). Nest fate was associated with trial ($G = 31.0$, df = 4, $P = 0.0000$), being lowest in trial 2 (7% of total nests disturbed) and highest in trials 3 (42%) and 4 (29%) for all sites combined. Nest fate also was related to site ($G = 24.4$, df = 2, $P = 0.0000$); disturbance rates were much higher at Cooper's Gap (38%) than at either Spruce Mountain (13%) or Turkey Hill (18%). Furthermore, disturbance rates were dependent on both trial and site considered concurrently ($G = 22.1$, df = 10, $P = 0.01$). In particular, disturbance rates at Cooper's Gap averaged 54% (range = 33–71%) during trials 3–5 compared to an average of 15% (range = 0–38%) during other trial-site combinations.

Discussion

Nest Predation Rates and Predator Communities

Predation rates observed in our study (23%) were comparable to those found elsewhere in other managed forests of Pennsylvania (22–24%) where abundance of avian predators, particularly American Crows, is low (Yahner et al. 1993; Yahner and Mahan 1996a). Moreover, predation rates in our study were similar to nest losses reported in studies of other gallinaceous birds, e.g., Spruce Grouse (*Falcipennis canadensis franklinii*; 17%) in boreal forests of Canada (Redmond et al. 1982). In contrast, when crow abundance is high, predation of artificial nests in forested landscapes is considerably higher (40–68%; Yahner and Scott 1988; Hogrefe et al. 1998). Hence, we attribute the greater predation rates at Cooper's Gap partially to higher abundances of crows. For example, during trials 3 to 5, 2.0

TABLE 1. Number of disturbed artificial ground nests in relation to distance from edge, time period (trial), and site in Rothrock State Forest, Huntingdon County, Pennsylvania (U.S.A.), 1998.

Variables	Levels	n	%
Distance from edge	50 m into retention stand	20	22
	at edge (0 m)	22	24
	50 m into adjacent forest	22	24
	150 m into adjacent forest	18	20
Time period	Trial 1	11	15
	Trial 2	5	7
	Trial 3	30	42
	Trial 4	21	29
	Trial 5	15	21
Site	Cooper's Gap	45	38
	Turkey Hill	16	13
	Spruce Mountain	21	18

crows/visit were recorded at Cooper's Gap compared to only 0.17 and 0.00 crows/visit at Spruce Mountain and Turkey Hill, respectively. A greater abundance of American Crows at Cooper's Gap in July-early August (trials 3–5) may be the result of crows becoming more gregarious, with family groups using this particular retention stand as a foraging site in summer subsequent to fledging of young (Gross 1946; Yahner and Wright 1985).

Predation rates in our study may have been different if our nests were baited with smaller eggs (e.g., Roper 1992; Haskell 1995). However, the experimental design of our study was to simulate nests of ground-nesting gallinaceous birds (Ruffed Grouse and Wild Turkey) in the region, thereby making brown chicken eggs a suitable substitute for actual eggs of these species (Yahner and Mahan 1996b). Use of these larger eggs likely precluded predation by smaller predators that might prey on smaller eggs of other ground-nesting birds in the retention stands, such as Eastern Towhee (*Pipilo erythrophthalmus*) (Haskell 1995; Blight et al. 1999).

Nest Predation Rates in Relation to Edge

As in most studies of artificial nests in forested landscapes (Yahner and Wright 1985; Rudnicky and Hunter 1993; Andrén 1995; Hartley and Hunter 1998), rates of nest predation in retention stands did not vary with distances from edges. Artificial ground nests in our study, regardless of distance from an edge, were well concealed by a dense layer of ground-level vegetation (usually > 70%, S. C. Talbott and R. H. Yahner, unpublished data), which likely reduced the foraging efficiency of predators and made these nests less susceptible to predation than aboveground (i.e., shrub) nests or those located in habitats with less dense vegetation near ground level (Bowman and Harris 1980; Sugden and Beyersbergen 1986; Yahner and Cypher 1987). Gradual edges created by ground-level vegetation and retention of trees of different size in retention stands probably reduced predation rates compared to higher rates that often occur at abrupt edges in forested landscapes (e.g., Suarez et al. 1997).

Although predation rates on ground nests did not differ with distances from edges per se, rates perhaps varied with differences in the degree of heterogeneity, i.e., extent of edges and amount of habitat contrast, within and among adjoining habitats in the local landscape. For instance, the Cooper's Gap site, with the highest predation rates in our study, was characterized by considerable induced and inherent edges (after Forman and Godron 1976) compared to the other two sites. The extent of induced edge at the Cooper's Gap site was increased by the retention of two 50-m wide, wooded corridors, which may have served as travel lanes or perching areas for foraging predators (Bergin et al. 1997; Yahner and Mahan 1997). An induced edge also was created by thinning in the adjacent forest along 10% of the downslope border of this retention stand. The inherent edge consisted of visible tree mortality caused by Gypsy Moth (*Lymnatria dispar*) defoliation along 20% of its upslope border prior to our study and a dense stand of Eastern Hemlock (*Tsuga canadensis*) along 5% of its downslope border. In contrast, Spruce Mountain and Turkey Hill stands had no wooded corridors and were proximal to relatively homogeneous stands of unharvested deciduous forest.

Support for our contention that nest predation rates within and adjacent to retention stands were associated with the degree of heterogeneity comes from other artificial nest studies. Higher predation rates were noted on nests located in forested landscapes affected by extensive clearcutting and containing considerable edge habitat compared to forested landscapes with less clearcutting and, hence, reduced edge habitat (Yahner and Scott 1988; Yahner and Mahan 1996a). Higher predation rates on nests also were found in forested fragments surrounded by agricultural habitats (i.e., appreciable habitat contrast) than in fragments surrounded by unharvested pine [*Pinus* spp.] stands (i.e., relatively less habitat contrast; Sargeant et al. 1998). Furthermore, an increasing number of studies are beginning to show that both localized and landscape-level factors can have a profound effect on avian predation rates (e.g., Bayne and Hobson 1997; Donovan et al. 1997; Rodewald 2000). In particular, forest stnds within fragmented agricultural landscapes have a greater number of generalist predators (e.g., corvids) than within more forested landscapes (Andrén 1992; Haskell 1995; Bayne and Hobson 1997).

A greater degree of heterogeneity in the landscape surrounding retention stands, which results from more extensive edge habitat or contrast with adjoining habitats, may enhance the abundance of some nest predators. American Crows, for example, are adapted to edge habitats (Whitcomb et al. 1981), and their abundance would be expected to be higher in forested habitat containing considerable edge habitat (e.g., Yahner et al. 1993). Furthermore, abundance of mammalian predators, like Raccoon, typically increase with greater amounts of edge and habitat diversity in the landscape (Heske 1995).

Management Implications

Our study suggests that rates of nest predation on ground-nesting gallinaceous bird species (e.g., grouse and turkey) in variable retention harvests of hardwood stands may not be related to distance of nests from edges per se but rather be a function of habitat heterogeneity in the surrounding landscape. Thus, we recommend future research on the effects of both wooded corridors and habitat heterogeneity on nest predation rates in these local landscapes. We caution, however, that we have presented no data on

predation rates of actual nests in retention stands to compare with our artificial nests.

Although this study represents the first published study of nest predation in retention stands, our data suggest that habitat conditions created by these stands may not have a major negative effect on the nesting success of common, ground-nesting gallinaceous birds. Additional additional artificial-nest studies associated with variable-retention systems in North America are needed, especially those with similar experimental design in order to better detect temporal and spatial trends across treatments or over time (Yahner 1996; Sargeant et al. 1998; Wilson et al. 1998).

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The Vascular Flora of Akimiski Island, Nunavut Territory, Canada

C. S. Blaney[1] and P. M. Kotanen[2]

Department of Botany, Erindale College, University of Toronto, 3359 Mississauga Road North, Mississauga, Ontario L5L 1C6, Canada
[1]Current address: Atlantic Canada Conservation Data Centre, PO Box 6416, Sackville, New Brunswick, E4C 4N1, Canada
[2]Correspondence author.

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The James Bay region is floristically little known. In this paper, we substantially expand and revise the flora of the largest of the James Bay islands: Akimiski Island, Nunavut Territory. We have added 76 taxa in 33 families, for a total of 276 native taxa and 5 exotics. In addition, we have updated taxonomy and have provided information on rarity. A large fraction of the plants on Akimiski are classed as uncommon or rare in Ontario; in many cases, these represent either coastal species, or species near their geographic range limits. Some may be threatened by climate change and habitat degradation.

Key Words: Akimiski Island, biodiversity, flora, global change, James Bay, Nunavut, Lesser Snow Geese.

Little detailed floristic information exists describing the coastal Hudson Bay Lowlands. Most of this region lies north or west of the area considered by the major eastern North American vascular floras (Gleason 1952; Fernald 1970; Gleason and Cronquist 1991; Marie-Victorin 1995), and south or east of the area primarily covered by Porsild and Cody (1980). The problem is acute for the Ontario coast and adjacent areas. The only flora to cover this region is Scoggan (1978), which contains little local detail. The lists of Morton and Venn (1990) and Newmaster et al. (1998) do include records from this region, but contain little or no information on geographic distributions, while Argus et al. (1982-1987) and Oldham (1999) include some distributional information but are solely concerned with rare species. The most detailed floristic publications specifically devoted to the James Bay region are Dutilly et al. (1958) and Riley and McKay (1980); more complete lists of Hudson Bay Lowlands plants with distributional maps also have been compiled by Riley (1980).

James Bay and Hudson Bay together represent a biogeographic region very distinct from the remainder of North America. Their low-latitude seacoasts are unique within the centre of the continent, and are isolated from the Hudson Strait, their connection to the Atlantic, by more than 10 degrees of latitude. Because climate zones dip south around Hudson Bay, this region contains habitats and species typical of much higher latitudes; for example, one of the southernmost mainland areas of sea-level tundra in the northern hemisphere is located on Cape Henrietta Maria, at the junction of James Bay and Hudson Bay. The paucity of published floristic information for this region not only represents a gap in our knowledge of North America's ecosystems, but also may hamper efforts to predict future threats to the biodiversity of the Hudson Bay Lowlands.

In this paper, we focus on the vascular plants of a single location: Akimiski Island, Nunavut Territory (including associated islets and shoals). This flora previously has been described by Riley (1981); we hope that our additions and revisions will make this one of the most complete floras for this region. Our work is significant not only because it adds substantially to existing knowledge, but also because the limited area and isolation of offshore islands limits rates of colonization and increases the risk of extinctions (e.g., MacArthur and Wilson 1967; Brown 1995). Our paper constitutes a record of current floristic diversity on this island, but this flora is likely to change substantially in future; we intend to create a record so that species lost or added in response to environmental changes may be recognized.

Methods

Study Site

Akimiski Island (53°N; 81°W; 2300 km^2) is the largest island in James Bay. It is separated from the Ontario mainland by the Akimiski Strait, which is about 20 km wide, but contains numerous shoals (Riley 1981; Martini 1984). The island is and its flora are geologically very young, having been exposed by the recession of the Tyrrell Sea about 3500-4000 years ago (Martini and Glooschenko 1984). This postglacial uplift is still occurring at a rate of about 0.7 cmyr^{-1} (Martini and Glooschenko 1984); as a result, new land is continuously being exposed, especially on the north and west sides of the island. With the exception of a few small outcrops of Palaeozoic limestones, the surficial geology of the island is dominated by marine silts and clays, generally covered with a peat layer, and interrupted by numerous gravel beach ridges (Martini and

Glooschenko 1984). The highest elevations are along the south coast, where the shore rapidly rises to about 60 m in elevation; in contrast, most other coastal areas are dominated by extensive, low-gradient marshes and mudflats (Martini and Glooschenko 1984). Sporadic permafrost exists in inland areas (Martini and Glooschenko 1984), where palsas and other permafrost features occur. Numerous large lakes are found near the south shore of the island, while linear marsh systems lie between the south shore and the first few beach ridges. Most rivers drain towards the north shore.

Akimiski Island lies within the boreal forest region. Regional vegetation is well summarized by Riley and McKay (1980), Riley (1981), and Martini and Glooschenko (1984). *Picea mariana*, *Picea glauca*, and *Larix laricina* forest are common throughout the island on beach ridges and as "islands" in peatland vegetation. Widespread shrub fens (largely *Salix* spp. and *Myrica gale*) occur close to the coasts, while graminoid-dominated peatlands occupy much of the island's interior. Dry tundra-like vegetation (e.g., *Saxifraga tricuspidata*, *Dryas integrifolia*) is found on exposed beach ridges, primarily along the north coast. Coastal salt marshes are most commonly dominated by *Festuca rubra* at higher elevations and *Puccinellia phryganodes*, *Carex subspathacea*, and *Glaux maritima* at lower sites, but in many areas these species are replaced by *Salicornia borealis* and *Spergularia canadensis*. A thematic vegetation map of the island has been prepared from LANDSAT TM data by Andrew Jano of the Ontario Ministry of Natural Resources (reference: AKIBAMP95).

Beaver formerly inhabited the island but are now apparently scarce, though abandoned dams are common. Resident populations of caribou and moose are absent. Parts of the north shore are used by a rapidly expanding breeding colony of Lesser Snow Geese; Canada Geese nest throughout the island (Abraham et al. 1999). Most of the island now falls within a federal Migratory Bird Sanctuary.

Akimiski Island has a limited history of human occupancy, with most impacts confined to coastal areas. Several Cree families from Ontario historically trapped and hunted on the island for extended periods of the year (K. Abraham, personal communication 1999). There are no villages on the island itself, but the island still is regularly visited by Cree from the Ontario shore, and there currently are some hunting camps near the west end. The only other structures on the island are associated with a research camp near Houston Point on the north shore, where studies of goose biology have been conducted by the Ontario Ministry of Natural Resources since the 1970s. A small Hudson Bay Company post once existed on the south coast, but its location is unclear (Riley 1981).

Sources of Information

Numerous collectors have visited the island, but typically for very short periods. The early history of botanical explorations is summarized by Riley (1981). Most of the collecting since that date has been associated with the Ontario Ministry of Natural Resources research camp on the north shore. In particular, Ken Abraham, Jennifer Bull, and Carol Lamey have collected and identified numerous specimens in the course of goose-related work; we have re-examined all of these specimens. In addition, in 1998, we had the opportunity to spend three weeks botanizing on the island; this represents the longest botanical collecting expedition in the history of Akimiski. Some additional collecting was done in 1999 and 2000 in association with other research by Peter Kotanen. Most of our collecting was performed in coastal areas (intertidal and supratidal marshes), but we also spent significant periods of time in freshwater habitats (mostly sedge and willow fens), and briefly visited remote areas in the interior and the east end of the island. Riley (1981) stated no "shallow marshes, beaver meadows, post-fire ridge systems, larch fens, black spruce swamp or thickets" had yet been sampled on Akimiski, and that "graminoid and lowshrub fens" had been very little sampled. We visited all of these habitats except spruce swamp, though we did examine several areas of spruce forest. Because of the high costs of helicopter travel, it is unlikely that any comparable expedition will happen in the near future.

Results

Our observations and collections have substantially increased the known flora of Akimiski Island, and have provided vouchers at the University of Toronto herbarium (TRT) for many new and previously reported taxa. We also have updated and revised the taxonomy of Riley's (1981) list; see Morton and Venn (1990) and Newmaster et al. (1998) for summaries of recent synonymy. A revised checklist is provided in Appendix A; this list has changed substantially from the 211 taxa in 51 families reported by Riley (1981). Taxonomic changes led to the removal of 6 taxa, which we consider to be synonymous with others on Riley's list, but our list also includes 76 additions in 33 families, for a new total flora of 281 species in 55 families.

We also have provided additional information on rarity and distribution. A high proportion of Akimiski taxa are classified as rare in Ontario (28 species: Newmaster et al. 1998; Oldham 1999); in many cases, these represent either coastal species or species near their southern range limits. As well, two Akimiski species currently are unknown from Ontario: *Potentilla crantzii* and *Salicornia borealis*. The taxonomically difficult *Potentilla crantzii* occurs not far to the north (Scoggan 1978; Porsild and Cody 1980); *Salicornia borealis* is found in

coastal regions of Hudson Bay (Wolff and Jefferies 1987).

Discussion

Riley (1981) speculated that 70 species could be added to the flora of Akimiski Island. Although our checklist adds more than this number, there is little reason to believe that this list is now complete. Further explorations of less-visited areas of Akimiski (especially the interior, the south shore, and both ends of the island) would undoubtedly yield additional species. Despite this, the current evidence suggests that diversity is lower on Akimiski than on the Ontario mainland. The Ontario coast south of the Attawapiskat River supports almost 450 vascular plant taxa (Riley 1980, 1981), and about 320 taxa are found north of Lake River on Cape Henrietta Maria (Riley and McKay 1980; Riley 1981), though diversity in the coastal areas closest to Akimiski is lower (Riley 1981). In contrast to the vascular flora, the lichen and bryophyte flora of Akimiski remain very poorly known, despite the great abundance of mosses and lichens in many habits; it is to be hoped that future research will address this gap in floristic knowledge.

Though smaller, the flora of Akimiski generally is similar to that of the Ontario mainland (Riley 1980; Riley and McKay 1980; Riley 1981). The large number of Akimiski taxa recorded as rare in Ontario probably reflects both the limited provincial distribution of tundra, treeline, and seacoast habitats, and the limited surveying of inland sites which has yet taken place; most are likely to occur in suitable mainland areas, such as Cape Henrietta Maria. As a result, the true degree of rarity of some of these species may be open to question. Similarly, few Akimiski species are likely to represent true range limits; instead, apparent distributional outliers often may represent species which occur in suitable habitats elsewhere within this region.

As is true of most remote northern floras (though not of transportation centres like Churchill: Scott 1996), the flora of Akimiski is almost entirely native, with only five clear exceptions (Morton and Venn 1990). Four of these (*Chrysanthemum leucanthemum*, *Plantago major*, *Sonchus arvensis*, *Taraxacum officinale*) are cosmopolitan weedy species; one (*Carum carvi*) probably was deliberately introduced by traders stationed at the Hudson Bay Company post (Riley 1981). None of these species is abundant. Morton and Venn (1990) also consider *Artemisia tilesii*, *Erysimum cheiranthoides*, *Potentilla norvegica*, and *Rhinanthus minor* to be introduced to Ontario, but these species are widespread in northern Canada, and at least northern populations are not treated as exotics by many authorities (Scoggan 1978; Porsild and Cody 1980; Newmaster et al. 1998; Voss 1972-1996; Cody 1996).

Although few exotics have yet colonized the island, in future the Akimiski flora is likely to suffer from two other types of impact. First, there is a significant risk that species will be lost as a result of global warming (Chapin et al. 1992). Northern ecosystems may be especially sensitive to climate change because small increases in temperature are expected to have significant effects on such important variables as snow cover, thaw depth, and peatland water tables (Maxwell 1992; Harvey 1997). As a result, like past climatic variation, future changes are likely to produce large shifts in treeline location, community composition, and ecosystem characteristics (Stevens and Fox 1991; Gates 1993). Akimiski lies not far to the north of the southern edge of permafrost; as temperatures rise, palsas and other permafrost-influenced landforms may be reduced or lost entirely (Maxwell 1992), to the detriment of species requiring drier or elevated microhabitats within the otherwise monotonous sedge fens that dominate the interior of the island (e.g., *Rubus chamaemorus*, *Cladina*). As well, though Akimiski is nearly 500 km south of the continental treeline in Keewatin or Québec, much of its flora has arctic affinities; such plants may be threatened by small increases in regional temperature. Akimiski may be especially at risk since many tundra species are already restricted to limited microhabitats (e.g., beach ridges, palsas), and since isolation from the mainland may both prevent these species from migrating as their habitat declines, and slow their replacement by species suited to a warmer climate.

A second set of impacts relates to geese. Considerable areas of coastal wetlands in the Hudson Bay region have been degraded by the foraging of rapidly increasing populations of Lesser Snow Geese (Jefferies 1988; Abraham and Jefferies 1997). The north shore of Akimiski was formerly used by thousands of staging Lesser Snow Geese during their migration to more northerly colonies (Abraham et al. 1999), and since 1968 has supported a nesting colony, currently numbering about 4000 birds (Abraham et al. 1999). Impacts are localized to areas heavily used by geese, but in these areas, many kilometres of the intertidal *Puccinellia phryganodes* zone and much of the supratidal *Festuca rubra* zone have been severely degraded, and some areas contain high densities of *Salicornia borealis* and *Spergularia canadensis*, which are indicative of severe goose damage (Srivastava and Jefferies 1996). Nearby fresh-water marshes also show signs of damage similar to those observed elsewhere on the Hudson Bay coast (Kerbes et al. 1990; Kotanen and Jefferies 1997). If the Akimiski colony continues to grow, it is probable that populations of sensitive coastal plant species will be locally reduced or lost, though most are likely to persist in less degraded areas.

In summary, this paper represents the most complete vascular flora yet compiled for Akimiski Island, and one of the more complete lists available for the James Bay region. More species inevitably will be discovered; however, results to date support the view that Akimiski has relatively low diversity compared to the mainland, as might be expected for an off-shore island. Currently, the flora of Akimiski includes numerous coastal and tundra species considered rare in Ontario, in addition to the many species typical of more southerly areas, but only a few exotics; if floristic changes do occur in future, this record represents a necessary first step towards their detection and documentation. Further work still is necessary to document the vascular flora of little-visited areas of the island, and to describe the diversity of other important taxa, particularly lichens and bryophytes.

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Appendix A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory

This checklist is based on Riley (1981), and includes plants of Akimiski Island and associated islets and shoals. Nomenclature follows Morton and Venn (1990); family order follows Newmaster et al. (1998); these publications also provide synonymy. Where names have changed from those of Riley (1981), the name used by Riley is given [in square brackets]. Additions from Riley (1980) are indicated by †; additions from Riley (personal communication 1990) by ‡; other additions are indicated by *. Taxa listed as extremely rare (S1), very rare (S2), or rare to uncommon (S3) in Ontario are indicated accordingly; "?" indicates questionable status (Newmaster et al. 1998; Oldham 1999). In addition, *Potentilla crantzii* and *Salicornia borealis* are not included in recent Ontario checklists (Morton and Venn 1990; Newmaster et al. 1998). Plants believed to be locally exotic are underlined.

Taxa represented in the University of Toronto herbarium are indicated by "TRT"; those in the herbarium of the National Museum of Natural Sciences, Ottawa by "CAN"; those in the herbarium of the Plant Biosystematics Institute, Agriculture Canada, Ottawa by "DAO". Specimens collected by Ken Abraham, Jennifer Bull, and Carol Lamey, and in the collection of Ken Abraham (Ontario Ministry of Natural Resources) are indicated by "K". Marc Johnson contributed *Galium trifidum* and *Goodyera repens*. Specimens for which the authors have collected vouchers are indicated by "V"; these have been deposited with TRT.

This checklist represents an ongoing project. Future revisions will be reported on the Akimiski Flora Web Page (http://www.erin.utoronto.ca/w3pkota/akiplants.html), maintained by P. M. Kotanen (Department of Botany, Erindale College, 3359 Mississauga Road North, Mississauga, Ontario, L5L 1C6, CANADA; pkotanen@credit.erin.utoronto.ca).

CHECKLIST

PTERIDOPHYTA		
Equisetaceae		
	Equisetum arvense L.	TRT,K,V
*	*Equisetum fluviatile* L.	V
	Equisetum variegatum Schleicer ex Fried. Weber & Mohr	TRT
Ophioglossaceae		
	Botrychium lunaria (L.) Sw.	TRT,V
	Botrychium minganense Victorin	K,V
SPERMATOPHYTA		
Gymnospermae		
Cupressaceae		
	Juniperus communis L. [var. *montana* Ait., var. *depressa* Pursh]	TRT,V
†	*Juniperus horizontalis* Moench	
Pinaceae		
	Larix laricina (Duroi) K. Koch	TRT
	Picea glauca (Moench) Voss [var. *glauca*, var. *porsildii* Raup]	TRT
	Picea mariana (Miller) Britton, Sterns & Pogg.	
‡	*Pinus banksiana* Lambert	

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Continued)*

Angiospermae		
Dicotyledons		
Ranunculaceae		
	Actaea rubra (Aiton) Willd.	
	Anemone canadensis L.	
	Anemone multifida Poiret ex Lam	TRT,K,V
*	*Anemone parviflora* Michaux	K
	Caltha palustris L.	TRT,K,V
*	*Ranunculus abortivus* L.	V
	Ranunculus cymbalaria Pursh	K
*	*Ranunculus gmelinii* DC. [*R. purshi* Richards]	K,V
S2	*Ranunculus hyperboreus* Rottb.	TRT
	Ranunculus macounii Britton	V
S2	*Ranunculus pedatifidus* Smith ex Rees	
*	*Ranunculus reptans* L.	V
*	*Ranunculus subrigidus* Drew	K,V
	Thalictrum venulosum Trel.	TRT
Myricaceae		
	Myrica gale L.	TRT,K
Betulaceae		
	Alnus incana (L.) Moench [*A. rugosa* (DuRoi)Spreng.]	
	Betula pumila L. [var. *glandulifera* Regel]	TRT,K,V
Chenopodiaceae		
*	*Atriplex cf. subspicata* (Nutt.) Rydb.	V
*	*Chenopodium capitatum* (L.) Asch.	K,V
*	*Chenopodium glaucum* L. ssp. *salinum* (Standley) Aellen	K,V
	Salicornia borealis S.L. Wolff & Jefferies [S. *europaea* L.]	V
S2	*Suaeda calceoliformis* (Hook.) Moq.	V
Caryophyllaceae		
	Honkenya peploides (L.) Ehrh.	TRT,V
	Minuartia dawsonensis (Britton) House	
	Moehringia lateriflora (L.) Fenzl [*Arenaria laterifolia* L.]	TRT,K,V
*	*Sagina nodosa* (L.) Fenzl	K,V
S2	*Spergularia canadensis* (Pers.) D. Don	TRT,DAO,V
	Stellaria borealis ssp. *borealis* Bigelow [*S. calycantha* (Ledeb.) Bong.]	TRT
S2S3	*Stellaria humifusa* Rottb.	TRT,K
	Stellaria longifolia Muhlenb. ex Willd.	TRT,K
	Stellaria longipes Goldie (s.l.)	TRT,K,V
Polygonaceae		
	Polygonum fowleri Robinson	TRT,K,V
	Polygonum viviparum L.	TRT,K,V
	Rumex occidentalis S. Watson	TRT,K,V
Sarraceniaceae		
*	*Sarracenia purpurea* L.	K
Droseraceae		
	Drosera anglica Hudson	TRT,V
*	*Drosera rotundifolia* L.	K,V
Violaceae		
*	*Viola nephrophylla* E. Greene	K,V
	Viola renifolia A. Gray	
Salicaceae		
	Populus balsamifera L.	TRT
‡	*Populus tremuloides* Michaux	
*	*Salix arctophila* Cockrell ex Heller	V
	Salix bebbiana Sarg.	V
	Salix brachycarpa Nutt.	TRT,K,V
	Salix candida Flüegge ex Willd.	K,V

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Continued)*

	Salix glauca L. ssp. *callicarpaea* (Trautv.) Böcher [*S. glauca* L. var. *callicarpaea* (Trautv.) Böcher]	TRT,K
S2?	*Salix myricoides* Muhlenb. [S. *glaucophylloides* Fern.]	TRT,V
	Salix myrtillifolia Andersson	K,V
*	*Salix pedicellaris* Pursh	V
*	*Salix planifolia* Pursh	K,V
*	*Salix reticulata* L.	V
*	*Salix serissima* (L Bailey) Fern.	V
Brassicaceae		
S2?	*Arabis arenicola* (Richardson ex Hook.) Gelert	K,V
*S2S3	*Cardamine pratensis* L. ssp. *angustifolia* (Hook.) O. Schulz	K
	Draba aurea M. Vahl ex Hornem.	TRT,K,V
	Draba glabella Pursh	CAN,K,V
	Draba incana L.	TRT,K,V
*	*Erysimum cheiranthoides* L.	V
	Rorippa palustris (L.) Besser ssp. *fernaldiana* (Butters & Abbe) Jonsell [*R. palustris* (L.) Besser ssp. *glabra* (Schulz) Stuckey var. *glabrata* (Lunell) Stuckey]	
Empetraceae		
	Empetrum nigrum L.	TRT,V
Ericaceae		
	Andromeda polifolia L. ssp. *glaucophylla* (Link) Hultén [*A. glaucophylla* Link]	TRT
	Andromeda polifolia L. ssp. *polifolia* [*A. polifolia* L.]	TRT,K,V
	Arctostaphylos alpina (L.) Sprengel [*A. alpina* (L.) Spreng. var. *alpina*]	TRT
	Arctostaphylos rubra (Rehder & E. Wilson) Fern. [*A. alpina* (L.) Spreng. var. *rubra* (Rehd. & Wils.) Bean]	K
	Arctostaphylos uva-ursi (L.) Sprengel [*A. uvaursi* (L.) Spreng. ssp. *uvaursi*, ssp. *adenotricha* (Fern. & Macbr.) Calder & Taylor]	TRT,V
*	*Chamaedaphne calyculata* (L.) Moench	K
	Gaultheria hispidula (L.) Muhlenb. ex Bigelow	TRT,V
*	*Kalmia polifolia* Wangenh.	V
	Ledum groenlandicum Oeder	TRT,K,V
*	*Vaccinium oxycoccos* L.	K,V
	Vaccinium uliginosum L.	TRT,V
	Vaccinium vitis-idaea L. ssp. *minus* (Lodd.) Hultén	TRT,K,V
Pyrolaceae		
	Moneses uniflora (L.) A. Gray	K
	Orthilia secunda (L.) House	TRT,K
	Pyrola asarifolia Michaux	TRT,K,V
	Pyrola chlorantha Sw.	
	Pyrola grandiflora Radius [*P. rotundifolia* L. ssp. *grandiflora* (Rad.) Andres.]	
Primulaceae		
	Androsace septentrionalis L.	TRT,CAN,K,V
S3?	*Glaux maritima* L. ssp. *obtusifolia* (Fern.) B. Boivin	TRT,K,V
	Primula egaliksensis Wormsk.	TRT,CAN,K,V
	Primula stricta Hornem.	TRT,K,V
	Trientalis borealis Raf.	TRT
Grossulariaceae		
	Ribes oxyacanthoides L.	TRT,V
	Ribes triste Pall.	
Saxifragaceae		
*	*Parnassia palustris* L.	K,V
	Parnassia parviflora DC.	TRT,V
	Saxifraga hirculus L.	TRT
	Saxifraga tricuspidata Rottb.	TRT,K,V
Rosaceae		
	Dryas integrifolia M. Vahl	TRT,K,V
	Fragaria virginiana Miller	TRT,K,V
	Geum macrophyllum Willd. [var. *perincisium* Rydb. Raup.]	V
	Potentilla anserina L. [var. *anserina*, var. *groenlandica* Tratt.]	TRT,V

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Continued)*

	Potentilla crantzii (Crantz) G. Beck.	
	Potentilla fruticosa L.	TRT
S2	*Potentilla multifida* L.	TRT,K
S2	*Potentilla nivea* L.	CAN
*	*Potentilla norvegica* L.	V
*	*Potentilla palustris* (L.) Scop.	K,V
	Potentilla pensylvanica L. [var. *pectinata* (Raf.) Lepage]	TRT,CAN,V
S2	*Potentilla pulchella* R. Br.	
	Rubus acaulis Michaux	TRT,K
	Rubus chamaemorus L.	TRT,V
Fabaceae		
	Astragalus alpinus L.	TRT,V
	Hedysarum alpinum L. [var. *americanum* Michx.]	TRT,V
	Hedysarum boreale Nutt. ssp. *mackenzii* (Richardson) Welsh [*H. mackenzii* Rich.]	CAN
	Lathyrus japonicus Willd. [*L. martimus* Willd. var. *pellitus* (Fern.) Gl.]	TRT,CAN,K,V
	Lathyrus ochroleucus Hook.	V
	Lathyrus palustris L.	K,V
S3	*Oxytropis viscida* Nutt. [var. *hudsonica* (Greene) Barneby]	
Elaeagnaceae		
	Shepherdia canadensis (L.) Nutt.	TRT,K,V
Haloragaceae		
*	*Myriophyllum sibiricum* Komarov	V
*	*Myriophyllum verticillatum* L.	K,V
Onagraceae		
	Epilobium angustifolium L.	TRT,K,V
*	*Epilobium ciliatum* Raf.	V
	Epilobium palustre L.	TRT,K,V
Cornaceae		
	Cornus canadensis L.	TRT,V
Santalaceae		
	Geocaulon lividum (Richardson) Fern. [*Comandra livida* Rich.]	TRT,K,V
Linaceae		
S2	*Linum lewisii* Pursh ssp. *lepagei* (B. Boivin) Mosq.	TRT,K,V
Apiaceae		
S1	*Carum carvi* L.	
*	*Cicuta bulbifera* L.	K,V
*	*Cicuta maculata* L.	K
*	*Cicuta virosa* L.	V
S3	*Ligusticum scoticum* L.	TRT,K,V
	Sium suave Walter	
Gentianaceae		
	Gentianella amarella (L.) Börner ssp. *acuta* (Michaux) J.M. Gillett	TRT,K,V
*	*Gentianopsis detonsa* (Rottb.) Ma s.l.	K
	Lomatogonium rotatum (L.) Fries ex Nyman	K,V
Menyanthaceae		
	Menyanthes trifoliata L. [var. *minor* Raf.]	TRT,K,V
Boraginaceae		
	Mertensia maritima (L.) Gray	TRT,K,V
Hippuridaceae		
*	*Hippuris tetraphylla* L.f.	K,V
	Hippuris vulgaris L.	TRT,K,V
Plantaginaceae		
	Plantago major L.	TRT
	Plantago maritima L.	TRT,CAN,K
Scrophulariaceae		
	Bartsia alpina L.	TRT
	Castilleja raupii Pennell	TRT,K
	Euphrasia hudsoniana Fern & Wieg. [*E. arctica* Lange]	K,V

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Continued)*

	Pedicularis groenlandica Retz.	TRT,V
	Pedicularis parviflora Smith ex Rees	TRT,V
	Pedicularis sudetica Willd.	TRT,V
S3	*Rhinanthus minor* L. [*R. cristagalli* L. (s.l.)]	TRT,K,V
Lentibulariaceae		
	Pinguicula vulgaris L.	TRT,V
	Utricularia intermedia Hayne	TRT
*	*Utricularia vulgaris* L.	V
Campanulaceae		
	Campanula rotundifolia L.	TRT,CAN
*	*Lobelia kalmii* L.	K
Rubiaceae		
	Galium labradoricum (Wieg.) Wieg.	TRT
*	*Galium trifidum* L.	
Caprifoliaceae		
	Linnaea borealis L. ssp. *longiflora* (Torrey) Hultén [*L. borealis* L. var *americana* (Forbes) Rehd.]	TRT,V
Valerianaceae		
	Valeriana dioica L. ssp. *sylvatica* (Sol. ex Rich.) F. Meyer [*V. septentrionalis* Rehd.]	CAN,V
Asteraceae		
	Achillea millefolium L. ssp. *borealis* (Bong.) Breitung [*A. millefolium* L. var. *nigrescens* Mey.]	K,V
	Achillea millefolium L. ssp. *lanulosa* (Nutt.) Piper [*A. millefolium* L. var. *occidentalis* DC.]	TRT
	Antennaria pulcherrima (Hook.) E. Greene	CAN,V
S1	*Antennaria rosea* E. Greene	K,V
	Artemisia campestris L. ssp. *borealis* (Pallas) H.M. Hall & Clements [*A. borealis* Pall.; *Artemisia canadensis* Michx.]	TRT,K,V
S2	*Artemisia tilesii* Ledeb. ssp. *elatior* (Torrey & A. Gray) Hultén	TRT,K,V
*	*Aster borealis* (Torrey & A. Gray) Prov.	K,V
S3?	*Aster brachyactis* S.F. Blake	TRT,V
	Aster longifolius Lam. [*A. johannensis* Fern.]	V
S3	*Chrysanthemum arcticum* L. ssp. *polare* Hultén	K
	Chrysanthemum leucanthemum L.	
	Erigeron acris L. [var. *asteroides* (Andrz. ex Bess.) DC.]	TRT,K,V
	Erigeron lonchophyllus Hook.	CAN,K
S3?	*Matricaria maritima* L. ssp. *phaeocephala* (Rupr.) Rauschert [*Tripleurospermum phaeocephalum* (Rupr.) Pobed.]	TRT,V
	Petasites sagittatus (Banks ex Pursh) A. Gray	CAN,K
	Senecio congestus (R. Br.) DC. [var. *palustris* (L.) Fern.]	TRT,K
	Senecio indecorus E. Greene	K,V
	Senecio pauperculus Michaux	TRT,K,V
*	*Solidago multiradiata* Aiton	K,V
	Solidago uliginosa Nutt.	TRT,V
*	*Sonchus arvensis* L. ssp. *uliginosus* (M. Bieb.) Nyman	V
	Taraxacum ceratophorum (Ledeb.) DC. (s.l.)	TRT,K,V
	Taraxacum lacerum E. Greene	TRT,V
	Taraxacum officinale G. Weber	TRT
Monocotyledons		
Scheuchzeriaceae		
*	*Scheuchzeria palustris* L.	K
Juncaginaceae		
	Triglochin maritimum L.	CAN,V
	Triglochin palustre L.	CAN,K,V
Potamogetonaceae		
	Potamogeton alpinus Balbis	CAN
	Potamogeton filiformis Pers.	K,V

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Continued)*

	Potamogeton gramineus L.	V
‡	*Potamogeton richardsonii* (A. Bennett) Rydb.	
Zannichelliaceae		
	Zannichellia palustris L.	CAN
Zosteraceae		
S2	*Zostera marina* L.	
Juncaceae		
	Juncus alpinoarticulatus Chaix [*J. alpinus* Vill.]	TRT,V
	Juncus balticus Willd. [var. *littoralis* Engelm.]	TRT,K,V
*	*Juncus bufonius* L.	K,V
*S3?	*Juncus castaneus* Smith	V
	Juncus triglumis L. ssp. *albescens* (Lange) Hultén	TRT,V
	Luzula parviflora (Ehrh.) Desv.	TRT
Cyperaceae		
S3	*Blysmus rufus* (Hudson) Link [*Scirpus rufus* (Huds.) Schrader var. *neogaeus* Fern.]	TRT,V
	Carex aquatilis Wahlenb.	TRT,K,V
	Carex aurea Nutt.	TRT,V
	Carex bigelowii Torr. ex Schwein	V
	Carex brunnescens (Pers.) Poiret ex Lam.	CAN
	Carex capillaris L.	TRT,K,V
*	*Carex capitata* L.	K,V
	Carex chordorrhiza Ehrh. ex L.f.	TRT
	Carex concinna R.Br.	CAN,V
	Carex diandra Schrank	TRT,V
*	*Carex flava* L.	V
*	*Carex garberi* Fern.	V
	Carex glareosa Schk. ex Wahlenb.	TRT,V
	Carex gynocrates Wormskj. ex Drejer	TRT,V
	Carex interior L Bailey	TRT,V
	Carex leptalea Wahlenb.	TRT,V
	Carex limosa L.	TRT,V
	Carex livida (Wahlenb.) Willd.	TRT,V
	Carex mackenziei V. Krecz.	TRT
*	*Carex magellanica* Lam.	V
*	*Carex microglochin* Wahlenb.	V
	Carex norvegica Retz. [C. media R. Br.]	
*	*Carex oligosperma* Michaux	K
	Carex paleacea Schreber ex Wahlenb.	TRT,K,V
S2?	*Carex praticola* Rydb.	V
*	*Carex rariflora* (Wahlenb.) Smith	V
*	*Carex rostrata* Stokes	K
*	*Carex saxatilis* L.	K,V
	Carex subspathacea Wormsk.	TRT,CAN,K,V
*	*Carex trisperma* Dewey var. *trisperma*	V
*	*Carex utriculata* F. Boott	K,V
	Carex vaginata Tausch	V
*	*Carex viridula* Michaux	V
*	*Eleocharis acicularis* (L.) Roemer & Schultes	V
*	*Eleocharis smallii* Britton	V
	Eriophorum angustifolium Honck.	TRT,CAN,V
	Eriophorum russeolum Fries ex Hartman	TRT,V
*	*Eriophorum tenellum* Nutt.	K
*	*Eriophorum vaginatum* L.	K
	Eriophorum viridi-carinatum (Engelm.) Fern.	TRT,V
	Kobresia simpliciuscula (Wahlenb.) Mackenzie	TRT
*	*Scirpus cespitosus* L.	V
*	*Scirpus hudsonianus* (Michaux) Fern.	V
Poaceae		
*	*Calamagrostis canadensis* (Michaux) P. Beauv.	V

(Continued)

APPENDIX A: Checklist of the Vascular Plants of Akimiski Island, Nunavut Territory *(Concluded)*

‡	*Calamagrostis stricta* (Timm) Koeler ssp. *inexpansa* (A. Gray) C.W. Greene	K,V
	Calamagrostis stricta (Timm) Koeler ssp. *stricta* [*C. stricta* (Timm) Koeler]	TRT,K,V
*	*Deschampsia cespitosa* (L.) P. Beauv.	V
	Dupontia fisheri R.Br. ssp. *psilosantha* (Rupr.) Hultén	TRT,K,V
	Elymus trachycaulus (Link) Gould in Shinn. ssp. *trachycaulus* [*Agropyron trachycaulum* (Link) Malte var. *trachycaulum*, var. *novae-angliae* (Scribn.) Fern.]	TRT,V
	Festuca brachyphylla Schultes & Schultes f.	TRT,K,V
	Festuca rubra L. ssp. *rubra*	TRT,K,V
	Festuca saximontana Rydb.	TRT, V
*	*Glyceria striata* (Lam.) A. Hitchc.	V
	Hierochloe odorata (L.) P. Beauv.	TRT,V
	Hordeum jubatum L.	TRT,K,V
	Leymus mollis (Trin.) Pilger [*Elymus mollis* Trin. ssp. *mollis*]	TRT,V
	Poa alpina L.	CAN,V
S2?	*Poa arctica* R. Br. ssp. *arctica*	CAN,K,V
	Poa glauca M. Vahl	TRT,V
	Poa palustris L.	
	Poa pratensis L. ssp. *alpigena* (Blytt) Hiit.	TRT
	Puccinellia lucida Fern. & Weath.	TRT,DAO
	Puccinellia phryganodes (Trin.) Scribn. & Merr.	TRT,CAN,K,V
	Trisetum spicatum (L.) Richter [var. *spicatum*]	TRT,K,V
Sparganiaceae		
	Sparganium angustifolium Michaux	V
*	*Sparganium natans* L.	V
Typhaceae		
*	*Typha latifolia* L.	V
Liliaceae		
	Maianthemum trifolium (L.) Sloboda [*Smilacina trifolia* (L.) Desf.]	TRT,K,V
	Tofieldia glutinosa (Michaux) Pers.	TRT,V
	Tofieldia pusilla (Michaux) Pers.	TRT,V
Iridaceae		
	Iris versicolor L.	TRT,K
Orchidaceae		
*	*Amerorchis rotundifolia* (Banks ex Pursh) Hultén	K,V
	Calypso bulbosa (L.) Oakes [var. *americana* (R.Br.) Luer]	
	Corallorhiza trifida Châtel	K
	Cypripedium passerinum Richardson	
*	*Goodyera repens* (L.) R.Br.	
S2	*Listera borealis* Morong	CAN
*	*Listera cordata* (L.) R.Br.	V
	Platanthera dilatata (Pursh) Lindley ex Beck	TRT,V
	Platanthera hyperborea (L.) Lindley	TRT,V
	Platanthera obtusata (Banks ex Pursh) Lindley	TRT,K,V
	Spiranthes romanzoffiana Cham.	TRT

Effects of Reopening Hunting on Survival of White-tailed Deer, *Odocoileus virginianus*, in the Bas-Saint-Laurent region, Québec

JEAN LAMOUREUX[1], MICHEL CRÊTE[2] and MATHIEU BÉLANGER[3]

[1]Société de la faune et des parcs du Québec, 212 avenue Belzile, Rimouski, Quebec, G5L 3C3, Canada
[2]Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, 675 boulevard René-Lévesque Est (BP 92), Québec, Québec, G1R 5V7, and Département de biologie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, Québec, G5L 3A1, and Département de biologie, Université Laval, Sainte-Foy, Québec, G1K 7P4, Canada
[3]Société de la faune et des parcs du Québec, 506 rue Lafontaine, Rivière-du-Loup, Québec, G5R 3C4, Canada

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Between 1996 and 1998, 59 White-tailed Deer (*Odocoileus virginianus*) in two major wintering areas in the Bas-Saint-Laurent region, Québec, were fitted with radio collars and followed using telemetry. The study period coincided with the reopening of hunting following three years of closure. Diminished deer numbers had been linked to severe winters intensified by Coyote predation. During the hunting moratorium, starvation, predation and vehicle collisions were the principal causes of deer mortality. Following the moratorium, hunting became the main cause of adult mortality (39% of known deaths) while starvation mostly affected fawns (13% of known deaths). Contrary to expectations, annual survival of adult females (0.73) did not differ statistically from that of adult males (0.66), despite firearm hunting being permitted only on adult males. It seems that accidental hunting and poaching of females in addition to bow hunting harvest lowered female survival rate and limited the possibility of population growth. Eastern Québec provides marginal habitat for deer due to severe winters. We thus conclude that maintenance of White-tailed Deer populations in this region requires strict adherence by hunters to hunting regulations, in addition to intensive management of wintering areas and supplementary feeding during harsh winters.

Key Words: *Canis latrans*, Coyote, *Odocoileus virginianus*, White-tailed Deer, hunting, mortality, poaching, population growth rate, survival, vehicle collision, Québec.

Entre 1996 et 1998, 59 cerfs de Virginie ont été munis de colliers émetteurs et suivis au moyen de la télémétrie dans deux des plus importantes aires de confinement de la région du Bas-Saint-Laurent au Québec. La période d'étude a coïncidé avec la réouverture de la chasse qui suivait un moratoire de trois ans rendu nécessaire par une diminution des effectifs reliée à des hivers rigoureux et aggravés par la prédation du coyote. Durant le moratoire sur la chasse, l'inanition, la prédation et les collisions automobiles avaient représenté les principaux facteurs de mortalité des cerfs. Après le moratoire, la chasse a constitué la principale cause de mortalité des cerfs adultes (39% des décès constatés) alors que l'inanition a surtout affecté les faons (13%). Contrairement aux résultats attendus, le taux de survie annuelle des biches (0,73) n'était pas statistiquement différent de celui des mâles adultes (0,66), malgré des modalités de chasse à l'arme à feu orientées seulement vers la récolte des mâles adultes. Conjugué à la récolte des archers, l'abattage des femelles, par erreur durant la saison de chasse à l'arme à feu, et par le braconnage a vraisemblablement diminué le taux de survie des biches et limité la possibilité d'accroissement de cette population. L'Est du Québec offre des conditions marginales d'habitat aux cerfs de Virginie à cause des hivers rigoureux. Nous concluons que le maintien de la population de cerfs dans la région nécessite un respect strict de la réglementation par les chasseurs en plus de l'aménagement intensif des aires d'hivernage et d'une alimentation d'urgence lors des hivers rigoureux.

Mots clefs: *Canis latrans*, Coyote, *Odocoileus virginianus*, Cerf de Virginie, braconnage, chasse, inanition, mortalité, survie, taux d'accroissement, Québec.

Winter harshness is the principal factor limiting White-tailed Deer (*Odocoileus virginianus*) populations occurring at the northern extremes of their distribution (Lamontagne and Potvin 1994; Dumont et al. 2000). During particularly severe winters in the early 1970s, mortality by starvation reached 40% in the Pohénégamook wintering area, Québec (Potvin et al. 1981). On Anticosti Island, winter mortality of adult females varied from 3 to 38% according to snow hardness (Potvin et al. 1997). Hunting is a secondary limiting factor in southeastern Québec because females have not been legally hunted with firearms since 1974 and deer populations can sustain an annual harvest of 5 to 10% of adult females and still increase in the absence of severe winters (Lamontagne and Potvin 1994).

The White-tailed Deer population of Québec's Bas-Saint-Laurent region declined rapidly in the early 1990s, following a series of severe winters. These harsh winters increased the influences of Coyote (*Canis latrans*) predation and loss of conifer canopy due to Spruce Budworm (*Choristoneura fumiferana*) in the traditional wintering areas (Dumont et al. 2000). The reduced deer numbers led

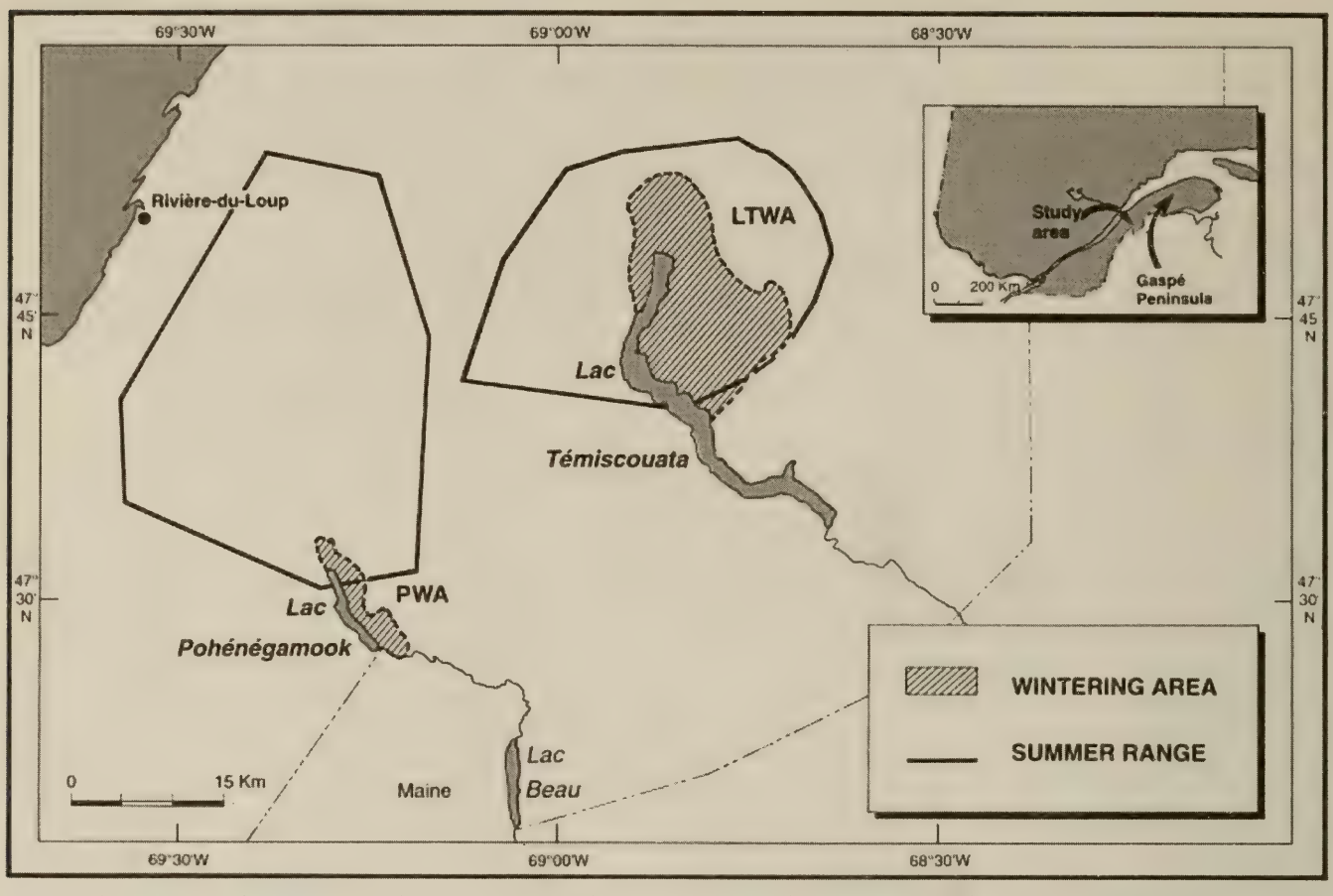

FIGURE 1. Map showing the two wintering areas and summer ranges for deer studied in the Bas-Saint-Laurent region, Québec.

to the closure of hunting in the region in 1993 and the institution of a recovery plan (MLCP 1992) which involved Coyote control in wintering areas, management of winter habitat and emergency feeding during harsh winters. At the same time, a research program was initiated to understand better the dynamics of this deer population. White-tailed Deer were thus fitted with radio collars and followed from the winter of 1994 in two of the largest wintering areas in eastern Québec, at Pohénégamook and Lac Témiscouata.

Between 1994 and 1996, starvation, Coyote predation and road accidents were the principal causes of deer mortality in the two wintering areas (Dumont et al. 2000). Competition for food appeared to regulate deer numbers at Pohénégamook while numbers of deer increased at Lac Témiscouata. The population as a whole recovered rapidly over the three years and hunting was reinstated in the fall of 1996.

Our objective in this study was to measure the effect of sport hunting on survival of deer at the northern limit of their distribution following reopening of the hunt by monitoring marked individuals for three years.

Study Area

The study took place in the Pohénégamook and Lac Témiscouata wintering areas, located approximately 40 and 55 km southeast of Rivière-du-Loup, respectively (Figure 1). Pohénégamook wintering area (PWA) (47°29′3″ N, 69°15′5″ W) covers 25 km^2 and is located approximately 40 km southeast of Lac Témiscouata wintering area (LTWA) (47°44′5″ N, 68°48′5″ W), which covers 221 km^2. Numbers of deer in the PWA in 1996 were estimated at 520 ± 62 deer (α = 0,10) using an aerial survey with double-count technique (Potvin et al. 1992), resulting in an estimated density of 20.7 ± 2.5 deer/ km^2. Numbers of deer in the LTWA in 1997 were estimated at 2166 ± 606 deer (α = 0,10), for an estimated density of 9.8 ± 2.7 deer/ km^2 (Dumont et al. 2000).

The two wintering areas occur in the mixed Balsam Fir/Yellow Birch forest type. Dominant tree species are Balsam Fir (*Abies balsamea*), White Spruce (*Picea glauca*), Eastern White Cedar (*Thuja occidentalis*), Trembling Aspen (*Populus tremuloides*) and Yellow Birch (*Betula alleghaniensis*). Due to the most recent Spruce Budworm outbreak in the late 1970s, the proportion of coniferous trees has been reduced (Dumont et al. 2000). Deer use all forest types during early winter but concentrate in mixed forests dominated by conifers (between 50 and 80 % coniferous canopy closure) during periods of heavy snow (Dumont et al. 1998). Both wintering areas are actively managed to optimize forest habitat for deer (MEF and MRN 1994, 1995).

Snow accumulation and sinking-depth conditions in the study area are among the most extreme for White-tailed Deer in Québec. The cumulative sinking-depth index (Potvin and Breton 1992) varied significantly over the study period for the two wintering areas. At PWA, winter conditions were mild in 1996 (2975 cm-days of sinking-depth), severe in 1997 (6380 cm-days) and near normal in 1998 (4443 cm-days). At LTWA, winter conditions were mild in 1996 (2242 cm-days) but severe in both 1997 (7291 cm-days) and 1998 (5257 cm-days).

The study area is located within Québec hunting zone number 2 and deer hunting regulations are relatively conservative. Bow hunting extends over 14 days and indiscriminate harvest of adult males, adult females and fawns is permitted. Bow hunters harvested 287, 316 and 321 deer in 1996, 1997 and 1998, respectively. The bow harvest consisted of 20% adult males, 42% adult females and 38% fawns. Firearm hunting extends over 16 days but only males with antlers of at least 7 cm in length may be taken. Total deer harvest, including bow hunting, was 1999, 1419 and 1354 deer in 1996, 1997 and 1998, respectively. Hunting was completely closed for three years between 1993 and 1995. Total harvest for the last year prior to the hunting moratorium was 352 deer in the fall of 1992.

Methods

White-tailed Deer were captured in January from 1994 to 1997 using modified Stephenson traps (Pichette and Samson 1975; Rongstab and McCabe 1984). Traps were placed near deer trails and baited with cedar twigs and commercial cattle feed. Captured deer were fitted with Holohil radio collars and followed from late September, 1996 to early December, 1998. Of the total 59 deer, 15 were fawns, 16 were adult (> 1 year old) males and 28 were adult females at time of capture. Forty-four deer were captured at PWA and 15 at LTWA. We located deer weekly during the study period using a Cessna 206 aircraft equipped with two Yagi antennae. For the period 1 May to 1 October, 1997, we located deer three times a week. When a collar emitted a stationary signal, we undertook a ground search to locate the animal and determine the cause of mortality, if the collar did not prove to have been lost. Using circumstantial evidence in the field (Dumont et al. 2000), we attributed death to one of the following causes : hunting, poaching, predation, starvation or road accident. Deer were considered poached if accidentally killed during the hunting season or illegally killed outside the season. Collars from legally harvested deer were taken by hunters to big game registration stations.

TABLE 1. Probability of various factors affecting survival rate of White-tailed Deer fitted with radio collars in the Bas-Saint-Laurent region in Québec, 1996-1998.

Factor	Univariate Test[a]	Multivariate Test[b]
Year	0.001	0.3001
Season	0.0002	0.0016
Age/Sex	0.047	0.0235
Area	0.6459	0.8188

[a]log-rank test of LIFETEST procedure (SAS 1988)
[b]likelihood-ratio test of GENMOD procedure (SAS 1988)

Statistical analysis

We calculated the daily probability of death (DPD) of White-tailed Deer using the GENMOD procedure of SAS (1988), assuming an exponential model. First we examined whether year, season, age/sex status (fawns, males > 1 year, females > 1 year) and wintering area affected survival rate of deer using both univariate and multivariate tests. The univariate analysis utilized a nonparametric log-rank test (LIFETEST procedure; SAS 1988) which has the advantage of not requiring a normal distribution; however, the log-rank test does not take into account other variables that could affect deer survival rate. The multivariate analysis was parametric; it utilized a likelihood-ratio test assuming the exponential model (GENMOD procedure; SAS 1988), which accounts for other variables when testing the effect of a specific variable. We tested whether the exponential model was appropriate by comparing it to the Weibull's model using a Lagrange multiple chi-squared test (LIFEREG procedure; SAS 1988). The exponential model does not take into account individual variation, as it assumes that all surviving animals have the same probability of dying at the beginning of the next time period.

We divided the year into four periods : winter (136 days; 6 December to 20 April), spring migration (10 days; 21 to 30 April), summer (approximately 149 days; 1 May to the beginning of the bow hunting season) and fall (approximately 70 days; beginning of the bow hunting season to 5 December). Bow hunting commenced on 28, 27 and 26 September in 1996, 1997 and 1998, respectively. Annual survival rate (ASR) was estimated by combining the four seasonal survival rates according to the following formula (Dumont et al. 2000):

$$ASR = (1\text{-}DPD_{win})^{136} \cdot (1\text{-}DPD_{spr})^{10} \cdot (1\text{-}DPD_{sum})^{149} \cdot (1\text{-}DPD_{fal})^{70}$$

The standard error of ASR can be estimated according to the formula (Agresti 1990):

$$SE(ASR)=ASR \cdot [136 \cdot SE(X_1)/(1\text{-}X_1) + 10 \cdot SE(X_2)/(1\text{–}X_2) + 149 \cdot SE(X_3)/(1\text{–}X_3) + 70 \cdot SE(X_4)/(1\text{-}X_4)]$$

where X_1, X_2, X_3 and X_4 represent DPD_{win}, DPD_{spr}, DPD_{sum} and DPD_{fal}, respectively.

Mortality rate due to hunting was estimated as the proportion of marked animals alive at the beginning

TABLE 2. Daily probability of death (DPD) and cause of mortality of radio-collared White-tailed Deer of differing age / sex status and at different seasons in the Bas-Saint-Laurent region in Québec, 1996–1998.

Age/Sex Status	Season	n[a]	DPD x10^{-3}	Standard Error x10^{-3}	Cause of Mortality					
					Predation	Hunting	Poaching	Starvation	Collision	Other[d]
Fawns	Winter	9	3.58	1.79				3	1	
Adult Males	Winter	14	0.45	0.30				1		1
	Spring	15	4.01	3.12						
	Summer	15	0.59	0.35						1
	Fall	19	3.31	1.23		7[b]				1
Adult Females	Winter	25	0.34	0.21						1
	Spring	26	3.06	2.28	1					1
	Summer	24	0.45	0.25			1			2
	Fall	30	2.52	0.78		5[c]	4		1	

[a]number of marked deer
[b]firearm hunting
[c]bow hunting
[d]indeterminate causes

of fall that was harvested. Confidence intervals were calculated using approximations generated from the binomial distribution and corrected for small sample size (Dixon and Massey 1969). DPD of adult males and adult females before and after the reopening of the hunt and of fawns and adults during winter were compared using Z- tests (Dixon and Massey 1969).

We calculated the finite population rate of increase (λ) of each of the wintering areas using matrix algebra according to the following formula:

$$\lambda = \frac{\lambda_1 + (\lambda_1^2 + 4\,\lambda_0\, f_1)^{1/2}}{2}$$

where λ_1 is the annual survival rate of adult females measured in this study, λ_0 is the annual survival rate of fawns (PWA = 0.34; LTWA = 0.48 : Dumont et al. 2000) and f_1 is the number of female offspring produced by yearling and older females (0.79 fawns/ adult female; Dumont et al. 2000).

Results

Univariate analysis revealed that year, season and age/sex status, but not wintering area, significantly affected the DPD of deer fitted with radio collars (Table 1). Multivariate analysis showed the same trends with the exception that year was no longer a significant factor (Table 1). Season and age/sex status clearly affected survival. Since the univariate analysis showed an annual variation in deer survival, we examined the data to find that survival was especially affected in the fall, a season for which we had three years of data. Because there were only two years of data for the other seasons, the sensitivity of the multivariate analysis was consequently reduced. We thus combined years in subsequent analyses. The exponential model was found to fit the data (Lagrange $\chi^2 = 0.098$, P = 0.75) and utilized to calculate the DPD.

DPD of radio-collared adult deer was seven to nine times higher during spring migration and fall than during winter and summer (Table 2). There was no significant difference between sexes in daily mortality rates for any season (two-tailed Z-tests, P > 0.05), especially in fall (Z = 0.54, P = 0.59), even though hunting mostly targetted adult males. For fawns, mortality was high during winter, although no data were available for other seasons. DPD of fawns during winter was significantly higher than that of adult males (Z = 1.70, one-tailed P = 0.04) and that of adult females (Z = 1.79, one-tailed P = 0.03). Overall winter survival rate of fawns was 0.61 (± 0.15) compared to 0.94 (± 0.04) for adult males and 0.95 (± 0.03) for adult females.

During the study period, hunting was the principal cause of mortality of adult deer (39% or 12 of 31 known deaths; see Table 2). Poaching accounted for 16% or 5 of 31 known deaths and 4 of these cases were adult females accidentally shot during the firearm hunting season. Starvation killed 13% (4/31) of marked animals, mostly fawns. Vehicle collisions

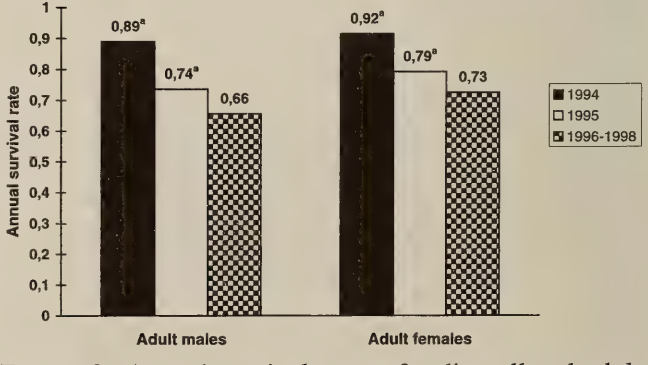

FIGURE 2. Annual survival rates of radio-collared adult males and adult females in the Bas-Saint-Laurent region, Québec, 1994-1998. [a] Dumont et al. 2000.

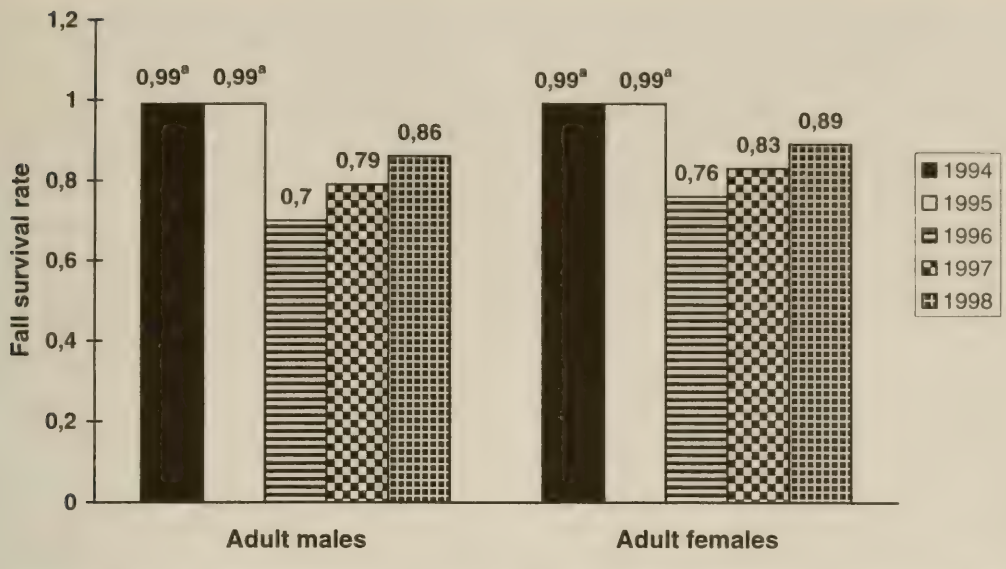

FIGURE 3. Fall survival rates of adult males and adult female White-tailed Deer in the Bas-Saint-Laurent region, Québec, 1994-1998. [a] Dumont et al. 2000.

(6%) and predation (3%) accounted for the remaining known deaths while 22% of mortality was of indeterminate cause (Table 2). Mortality rate due to hunting, including wounding and errors, was 0.17 (0.11 – 0.27, $\alpha = 0.05$) for both sexes combined. During the same period, the harvest rate of adult males was 0.23 (0.10 – 0.42, $\alpha = 0.05$).

We calculated annual survival rate for adult males and adult females by combining measured survival rates for each season. Since the multivariate analysis did not reveal differences between years or areas, we calculated an overall mean for each sex. Annual survival rate from 1996 to 1998 was 0.66 (± 0.14) for adult males and 0.73 (± 0.10) for adult females. These rates are much lower than those measured between 1994 and 1995 (Dumont et al. 2000), when hunting was closed (see Figure 2). Fall survival rate dropped sharply with the reopening of hunting from 0.99 to 0.70 for adult males and from 0.99 to 0.76 for adult females (see Figure 3).

Using measured survival rates of deer, we estimated finite population rate of increase (l) between 1996 and 1998 to be 1.00 at PWA and 1.08 at LTWA. The value found for the PWA is similar to those recorded during the hunting moratorium while the hunted population growth rate found for the LTWA was lower than those reported before hunting reopening (Dumont et al. 2000).

Discussion

Hunting was the principal cause of mortality of radio-collared adult deer in the Bas-Saint-Laurent region following reopening of the hunt. It was noteworthy that hunting and poaching significantly reduced annual survival rate of adult females because firearm hunting was only permitted on adult males. In addition, the fall DPD did not differ significantly between the two sexes over three years. Under similar hunting restrictions in New Brunswick and Michigan, hunting and poaching mortality rates varied between 1.6 and 4% for adult females (Whitlaw et al. 1998; Van Deelen et al. 1997). Mortality rates due to hunting and poaching reached 16 % in our study. This level of additive mortality seemed to reduce adult female survival to such an extent that the population growth rate was curbed to 1.00 at PWA and 1.08 at LTWA, despite relatively mild winters. Numbers of adult males harvested with firearms within the entire hunting zone did not vary much from 1997 (1102) to 1998 (1032), which also suggests a relatively stable population.

The annual survival rate of adult males in our study (0.66) was slightly higher than the 0.57 reported for northern New Brunswick between 1994 and 1997 (Whitlaw et al. 1998) and the 0.51 for Nova Scotia between 1994 and 1998 (Patterson 1999). Adult male survival rates can be as low as 0.22 in heavily hunted populations (Van Deelen et al. 1997) and thus our findings for males do not cause concern. The annual survival rate of adult females of 0.73, however, was lower than that found in other studies, e.g., 0.85 in New Brunswick and 0.80 in Nova Scotia, and resulted from identification errors during the firearm hunting season and from poaching. Illegal killing of female deer accounted for as much mortality as did legal bow hunting (Table 2). Illigal killing also represented a major mortality factor for adult female Mule Deer (*Odocoileus hemionus*) in western USA (McCorquodale 1999). Overwinter fawn survival averaged 61% during our study, in comparison to 52 – 84% for the same two populations during the moratorium on hunting (Dumont et al. 2000). Winter fawn survival slightly exceeded 60% during the same period in New

Brunswick and varied between 51 and 61% in Nova Scotia (Ballard et al. 1999; Patterson 1999). Fall survival rates tended to increase over the three years for both sexes of adults, but not significantly (Figure 3). This may be because the animals marked at the beginning of our study had aged and gained experience that would reduce the risk of being killed during the hunt. In addition, it is possible that deer modified their behaviour to lessen their vulnerability to hunting, as previously reported elsewhere (Kilgo et al. 1998).

Besides hunting, starvation, collision and predation remained the major mortality factors of deer during our study, as Dumont et al. (2000) previously observed. This contrasted with mortality causes of White-tailed Deer in New Brunswick and Nova Scotia where Coyote predation strongly dominated and starvation passed almost unobserved (Whitlaw et al. 1998; Ballard et al. 1999; Patterson 1999). Methodological differences in identifying mortality causes may partly be involved in such differences (see Dumont et al. 2000 for the criteria we used), but other factors likely explained this discrepancy. The reduced occurrence of Coyote predation in our study area could result from lower Coyote densities in south-eastern Québec than in New Brunswick and Nova Scotia. Coyote density averaged 0.5 animal/10 km^2 in the forest landscape of our study area, where most deer stayed year-round, in comparison to 2,7 coyotes/10 km^2 in the rural landscape (Richer 2000). No figures on Coyote density existed for the Maritimes, but a greater proportion of cultivated land in New Brunswick or Nova Scotia would likely result in higher Coyote density; milder winters in the Maritimes could also increase the carrying capacity for coyotes if they facilitated Coyote survival or fecundity. Depressed Coyote density in Québec could otherwise originate from high harvest rates by trappers, which varied between ≈ 40-60% during the last decade (Crête and Lemieux 1996; unpublished). Lower incidence of Coyote predation in Québec could finally depend on deer density in winter and on location of deer home range within wintering areas; generally, deer wintering in small groups or at the periphery of wintering areas are more vulnerable to Coyote predation than those occupying large wintering areas (Messier and Barrette 1985; Brundige 1993; Patterson and Messier 2000).

Reopening of sport hunting led to a sharp decline in annual survival of adult female White-tailed Deer in the Bas-Saint-Laurent region, even though only the harvest of antlered males was permitted during the firearm season. Accidental or deliberate killing of adult females was sufficient to limit the population growth rate in this region situated at the northern limit of the species' distribution. It is therefore important that hunters be made aware of the negative consequences of illegal hunting. In the long term, managers should also assess the effect of harvesting adult females through bow hunting, given the increasing popularity of this activity in Québec. Bow hunting represented 24% of the total regional harvest in 1998 compared to 8% in 1990, while fully 42% of deer taken by bow hunters in recent years were adult females. These results lead us to conclude that the White-tailed Deer population in eastern Québec requires strict adherence of hunters to hunting regulations, in addition to supplemental feeding during harsh winters and intensive management of wintering areas.

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Slumping Activity and Forest Vegetation Along the Northeastern Shore of Waskesiu Lake, Prince Albert National Park, Saskatchewan

D. H. DE BOER and O. W. ARCHIBOLD

Department of Geography, University of Saskatchewan, 9 Campus Drive, Saskatoon, Saskatchewan, S7N 5A5, Canada

De Boer, D. H., and O. W. Archibold. 2001. Slumping activity and forest vegetation along the northeastern shore of Waskesiu Lake, Prince Albert National Park, Saskatchewan. Canadian Field-Naturalist 115(1): 106–114.

Changes in forest cover along the shore of Waskesiu Lake, Saskatchewan, can be related to slumping. This study evaluates the impact of slumping along the lakeshore on the structure of the vegetation. The oldest trees in the undisturbed forest were approximately 100 years old, whereas the trees which had established on recent scars were typically less than 10 years old. Tree rings were used to determine the ages of the reaction wood in bent trees that had survived the disturbances; this indicated that recent slumping events occurred in 1973, 1979, and 1984. These years either received higher than normal precipitation or had above normal lake levels. Recent slope disturbances were characteristically colonized by a sparse cover of herbaceous plants and tree seedlings which contrasted with the adjacent slopes which supported a mixed forest cover dominated by White Spruce, Balsam Fir, and Paper Birch. Herbaceous ground cover on the slumps was composed of 35 herb and grass species compared to 14 species on the intervening slopes. Similarly, the shrub cover was more diverse on the slumps (9 species) than on the adjacent slopes (4 species). The greatest density of herbs and grasses occurred near the base of the slumps, where soil moisture conditions were more suitable for plant growth. Slumping is most likely caused by subsurface seepage, with annual fluctuations in lake level and seasonal wave activity possibly contributing to the process. As well as causing higher lake levels, wet years can also promote slope instability by increasing the water content of the surficial materials. However, there is no simple relationship between precipitation, temperature, lake level and the occurrence of slumping.

Key Words: White Spruce, *Picea glauca*, dendrochronology, reaction wood, shoreline instability, slumping, Waskesiu Lake, Saskatchewan.

Vegetation can provide useful evidence of the frequency of occurrence and rates of geomorphic disturbance. Avalanche tracks, for example, are readily apparent in mountains because of the local absence of large trees on otherwise forested slopes. Estimating avalanche frequency was one of the earliest applications of dendrochronology (Sherzer 1905). Other forms of mass wasting, such as debris flows and landslides, also have been dated in this way (Shroder 1978; Yamaguchi and Hoblitt 1995; Yoshida et al. 1997). Rates of river channel migration (Gottesfeld and Gottesfeld 1990) and river flood frequencies (Everitt 1968) have been inferred from intra-ring abnormalities which appear as zones of enlarged vessels (Yanosky 1983). Similarly, chronologies of shoreline processes resulting from ice-push activity, wave action and lake level fluctuations induced by variations in precipitation have been established from tree growth patterns (Alestalo 1971; Begin and Payette 1988; Lepage and Begin 1996).

Slumping and earth flows frequently create characteristic features that can be recognized by their vegetation cover which contrasts with that of the surroundings. The extent of the slump is well defined initially, but becomes progressively masked as vegetation reestablishes at the site. Nevertheless, comparatively recent slope activity in forested areas may still be detected by differences in the age and structure of the plant cover. In addition, slope instability can cause trees to tilt. Reaction wood with distinct cellular structure is subsequently produced in the trunk in an attempt to restore the erect habit (Braam et al. 1987). Reaction wood in conifers forms on the compression side of the bend and favors the development of wider annual rings on that side of the trunk, which results in eccentric cross sections. Reaction wood is often darker than normal wood. Such deformities can provide dendrochronological evidence of slumping.

Tilted trees are found at various points along the northeastern shore of Waskesiu Lake, Saskatchewan in conjunction with slope failures (Figure 1). The purpose of the present study was to evaluate the impact of slumping along the lakeshore on the community structure of the vegetation, and to relate slumping events to lake level fluctuations using tree ring data.

Study Area

Waskesiu Lake is located in the east central part of Prince Albert National Park in northern Saskatchewan (53°57′N, 106°15′W). This area was heavily glaciated and ice retreat occurred approximately 11 500 BP (Padbury et al. 1978). The lake basin and surrounding area consist of Wisconsin age tills and associated deposits at least 90 m thick. The tills are typically soft and unjointed, and consist of

FIGURE 1. Characteristic bent trunks in White Spruce trees growing in slope failure sites along the northeast shore of Waskesiu Lake.

non-stratified deposits of boulders, gravels, sands, silts and clays. Veneers of stratified deposits of glaciofluvial, fluvial, and lacustrine origin are locally present.

The drainage area of the Waskesiu Lake watershed is approximately 500 km^2 and the surface area of lake is 68.3 km^2 (Gimbarzevsky 1973). Annual precipitation averages 455.7 mm, of which 32% falls as snow from October to April (Atmospheric Environment Service 1993). Rapid snowmelt, which normally occurs over a two-week period in late April, is an important feature of the hydrologic regime of the area. Water levels typically peak in June and July in response to snowmelt and summer thunderstorms. Humans have affected water levels of Waskesiu Lake in various ways since European settlement. Diversion of Beartrap Creek, an influent stream, occurred as early as 1915. In 1936 a weir was constructed on the Kingsmere River where it enters Waskesiu Lake; this was designed to raise the water level in a section of rapids to facilitate boating in the National Park which was established in 1927. In 1938, the Beartrap Creek diversion was removed in an attempt to raise water levels following the drought years of the 1930s. The following year a dam was built near the head of the Waskesiu River where it exits Waskesiu Lake to improve boat access to the town site wharf (Anions and Beaven 1988). By 1941 water levels were so low that the dam was not functional (Rogers 1941), but in 1942 water levels had risen by as much as 0.75 m (Kooyman 1980). In 1962-1963 a new marina was constructed. To accommodate this facility, the dam on the Waskesiu River was upgraded and the lake level increased to an elevation of 532.18 m above sea level (Environment Canada 1989) compared to the pre-impoundment elevation of Waskesiu Lake of 530.3 m above sea level (Rawson 1936). There has been no set policy governing regulation of water levels in the park, and for the period of record (1954-1993) lake level has fluctuated by approximately 1 m (Figure 2). A weir on the Kingsmere River midway between Kingsmere Lake and Waskesiu Lake was removed in 1999.

The site is located in the Mixedwood Forest Section of the boreal forest (Rowe 1972). The characteristic vegetation is mixed stands of White Spruce (*Picea* glauca) and Trembling Aspen (*Populus tremuloides*), with White Birch (*Betula papyrifera*), Balsam Poplar (*Populus balsimifera*) and Balsam Fir (*Abies balsamea*) locally present. The dominant soils in the area are shallow, medium-textured Luvisols with clayey B-horizons overlying sandy parent materials.

Along the northeastern section of the lakeshore the land rises abruptly with slopes of 20° to 40° ter-

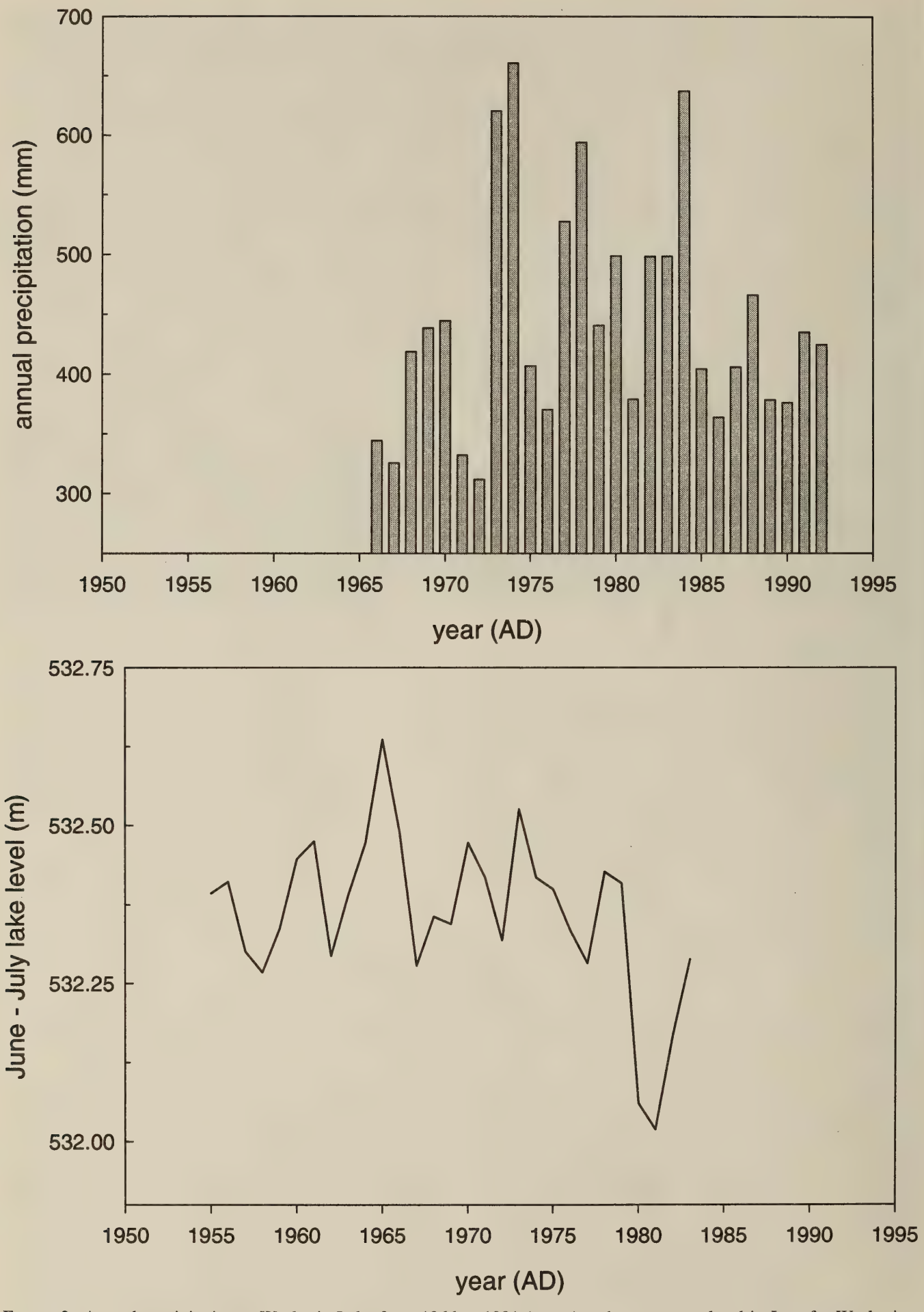

FIGURE 2. Annual precipitation at Waskesiu Lake from 1966 to 1991 (upper) and mean water level in June for Waskesiu Lake for the period 1954 to 1983 (lower).

TABLE 1. Circumference and age of trees in forest and on the perimeter of slump sites along the shore of Waskesiu Lake.

	Circumference (cm)				Age (y)			
	Mean	S.D.	Max	Min	Mean	S.D.	Max	Min
Undisturbed forest								
Balsam Fir	36.5	12.3	54	17	46.7	9.4	67	21
White Spruce	65.2	29.3	117	24	72.9	22.3	98	44
White Birch	55.1	21.0	94	27	80.6	11.7	98	67
Perimeter of slumps								
Balsam Fir	34.8	15.5	56	15	30.2	11.6	46	12
White Spruce	54.6	34.9	135	15	38.3	21.6	88	10
White Birch	60.8	25.4	117	17	76.4	16.7	89	30
Trembling Aspen	54.0	7.9	64	45	72.8	9.7	81	58

minating in a pronounced convexity at the upper end of the slopes. The difference in elevation between the lake surface and the crest of the slopes ranged from 10 to 25 m and the horizontal distance from the shoreline to the crest varied from 25 to 55 m. Further inland a boggy depression has formed which acts a cistern for water draining through the surface material towards the lake. Wave action has produced a low ridge of coarse boulders eroded from the glacial till along the base of the slopes, approximately 2.5 m wide and up to 1.5 m high. At the shoreline, cone-shaped slumps have developed, varying from 10.3 m to 39.8 m in width, with a sparsely colonized, sandy substrate that contrasts with the adjacent forested slopes.

Methods

Eleven recent slumps and four intervening, stable sites were selected for detailed investigation. Transects were located along the length of the slopes at right angles to the shoreline. The tree cover was assessed from 5 m-wide belt transects in which all individuals were noted for species and trunk circumference. Tree core and trunk diameter data were collected from 250 trees growing on the slumps and in the undisturbed forest beyond the influence of slumping. The rings were counted under a low-power binocular microscope and used in conjunction with tree diameter to establish a general age-size relationship that could be applied to the different species growing in the study area.

Cores from selected White Spruce trees were analyzed in detail to evaluate the temporal changes in ring width. White Spruce was chosen because it was ubiquitous in the field area, and because its rings were easily visible and well preserved throughout the whole length of the core. Ring widths were measured for 28 White Spruce growing in the forest; the oldest of these provided a growth record back to 1897. An additional 41 White Spruce growing at the perimeter of the slumps also were measured and provided a growth record back to 1904.

At one site with recent slumping, five trees with marked trunk curvature were felled and sectioned into 1 m lengths for detailed ring analysis including assessment of annual ring widths and eccentricity of growth. The sample size was restricted by Parks Canada in order to minimize disturbance of the lakeshore forest. The age at which reaction wood developed was noted, and is assumed to be the date at which slumping occurred. Tree ring chronologies were subsequently compared to lake level and annual precipitation records.

Results and Discussion

The oldest White Spruce trees in the mature forest beyond the crest of the slope were approximately 100 years old. The oldest White Birch were of a similar age, although Balsam Fir was typically less than 50 years old. This area was burned about 100 years ago, and the age of the tree cover is consistent with the fire history and ecology of the dominant species. The circumferences and ages of the conifers growing in the forest are presented in Table 1. Circumferences ranged from 36.5 ± 12.3 cm for Balsam Fir to 65.2 ± 29.3 cm for White Spruce; this corresponded to a mean age of 47 ± 9 years and 73 ± 22 years, respectively. For White Birch mean circumference was 55.1 ± 21.0 cm giving a mean age of 81 ± 12 years. The average tree density in the forest was 3160 individuals ha^{-1}.

On the intervening slopes between the slumps, average tree density ranged from 1950 ± 174 individuals ha^{-1} at the shoreline to 4300 ± 240 individuals ha^{-1} at 30-40 m from the lake. Balsam Fir was the most abundant species on these slopes and accounted for 54% of the tree cover compared to 32% for White Spruce, 8% for White Birch and 6% for Trembling Aspen. The oldest White Birch on the intervening slopes was aged at 89 years, compared to 88 years for White Spruce, 81 years for Trembling Aspen, and 46 years for Balsam Fir. Species common to the boreal forest, such as Hazel (*Corylus cornuta*), Twinflower (*Linnaea borealis*) and Two-

TABLE 2. Density (individuals/m^2) of ground cover species on recent slumps and intervening slopes.

	slumps							intervening slopes
	0m	10m	20m	30m	40m	50m	total	total
Herbs and grasses								
Achillea sibirica	0.5						0.5	
Anemone canadensis	1.7						1.7	
Apocynum androsamifolium		0.1					0.1	
Arabis holboeillii		0.4	0.1				0.5	
Aralia nudicaulis	1.8	1.3	0.6	3.2	3.3	1.6	11.8	8.5
Artemisia abronatum	0.5	0.4	0.3				1.1	
Artemisia absinthium	1.8	2.5	5.1			0.4	9.9	
Aster ciliolatus	0.4	2.1	0.1	5.7			8.3	4.3
Aster conspicuus	1.5	2.3	0.5	1.5	1.3		7.1	4.5
Aster erocoides			0.1				0.1	
Aster hesperius	4.3	0.1		0.1			4.5	8.0
Campanula rotundifolia	0.8	1.0	1.6	0.1			3.5	
Cicuta maculata	2.3						2.3	
Cirsium arvense	0.8						0.8	1.8
Cornus canadensis		0.1		1.5	0.9		2.5	
Elymus innovatus	0.8	3.0	3.8	0.5	1.6		9.7	
Equisetum arvense	22.9	2.1					25.0	
Equisetum hyemale	1.3						1.3	
Erigeron philadelphicus	0.1						0.1	
Fragaria vesca		0.7		0.3	3.2		4.2	4.8
Fragaria virginiana			0.5				0.5	
Galium borealie	1.7	4.2	14.7	9.4	2.4		32.4	3.5
Lathyrus ochroleucus	1.2	1.7	3.4	2.2	2.8	1.2	12.4	0.8
Lathyrus venosus		0.8	0.4	0.9			2.1	
Linnaea borealis				0.1			0.1	6.5
Maianthemum canadense	0.8	0.4	1.5	6.5	5.1	3.8	18.0	5.8
Mentha arvensis	3.7						3.7	2.8
Parnassia palustris	2.0						2.0	4.3
Solidago candensis	5.8	2.3	0.8				8.9	0.5
Solidago sp.	1.3	0.1	2.3				3.6	
Sonchus arvensis	6.0						6.0	
Stachys palustris	0.2						0.2	
Thalictrum venulosum	0.7	0.8					1.5	
Urtica dioica	0.6		0.1	0.5			1.2	
Vicia americana	1.6	4.7	4.8	2.2	1.4		14.8	0.5
total herbs	67.2	31.0	40.5	34.6	22.1	7.0		
Shrubs								
Actaea rubra	0.1	0.6	1.8	0.5	0.4		3.5	0.8
Alnus rugosa	0.1	0.7	0.2				1.0	
Amelanchier alnifolia	0.2	1.0	2.2	0.4			3.7	
Corylus cornuta			0.4	1.1	0.4		1.9	10.3
Ribes americanum	0.7		0.1		1.0		1.8	
Rosa acicularis	1.3	6.6	6.5	3.7	2.6		20.6	6.3
Rubus strigosus	0.9		0.1	1.4	2.2		4.6	
Symphoricarpos albus	0.3	2.5	0.3	0.9			4.0	2.3
Symphoricarpos occidentalis		0.6	0.2				0.8	
total shrubs	3.5	12.2	11.6	8.0	6.7			

leaved Solomon's seal (*Maianthemum canadense*), as well as those typically associated with open or disturbed sites, for example Canada thistle (*Cirsium arvense*) and Rose (*Rosa acicularis*) were present in the understory (Table 2). The groundcover at these sites was composed of 14 species of herbs and grasses and 4 species of shrubs.

Vegetation cover was extremely variable on the slumps. Average tree density adjacent to the shoreline was 2441 ± 1922 individuals ha^{-1}, and decreased progressively away from the shoreline to 1195 ± 668 individuals ha^{-1} at a distance of 10-20 m and 672 ± 498 individuals ha^{-1} at the head of the scars at a distance of 30-40 m. White Spruce was the most abun-

TABLE 3. Percent composition, circumference and age of trees growing on the recent slump sites

	0-10 m	10-20 m	20-30 m	30-40 m	Total
Number of individuals					
Balsam Fir	6	8	6	1	21
Balsam Poplar	3	6	6	2	17
Trembling Aspen	0	7	3	14	24
White Birch	13	5	1	0	19
White Spruce	55	13	12	16	96
Percent composition					
Balsam Fir	7.8	10.4	7.8	1.3	11.9
Balsam Poplar	3.9	7.8	7.8	2.6	9.6
Trembling Aspen		9	3.9	18.2	13.6
White Birch	16.9	6.5	1.2	0	10.7
White Spruce	71.4	16.8	15.5	20.7	54.2
Trunk circumference (cm)					
Balsam Fir	9.8 ± 7.2	11.4 ± 4.1	14.5 ± 11.6	4.5*	
Balsam Poplar	38.0 ± 46.6	5.4 ± 3.1	4.1 ± 0.9	2.5 ± 0.7	
Trembling Aspen		4.6 ± 1.8	2.9 ± 1.6	67.7 ± 10.3	
White Birch	65.3 ± 26.0	38.3 ± 31.6	60*		
White Spruce	33.7 ± 32.4	5.4 ± 3.1	4.1 ± 0.7	2.5 ± 0.7	

*one individual

dant tree species on the scars and accounted for 54% of the individuals compared to 13% for Trembling Aspen, 12% for Balsam Fir, 11% for White Birch and 10% for Balsam Poplar (Table 3). A total of 35 herb and grass species was present on the slumps. Northern Bedstraw (*Galium borealie*) was the most abundant (32.4 individuals/m^2) with Horsetail (*Equisetum arvense*), Two-Leaved Solomon's Seal, American Vetch (*Vicia americana*) and Wild Sasaparilla (*Aralia nudicaulis*) also common (Table 2). The greatest density of herbs and grasses occurred near the base of the slumps (67.2 individuals/m^2) and density decreased to 7 individuals/m^2 at the slump heads. The general increase in herbaceous cover on the lower part of the slumps is related to moisture seeping into the exposed sandy substrate and the near-surface water table along the shoreline. Nine species of shrubs were growing on the slumps. Prickly rose (*Rosa acicularis*) was the dominant shrub (20.6 individuals/m^2). Other species, including

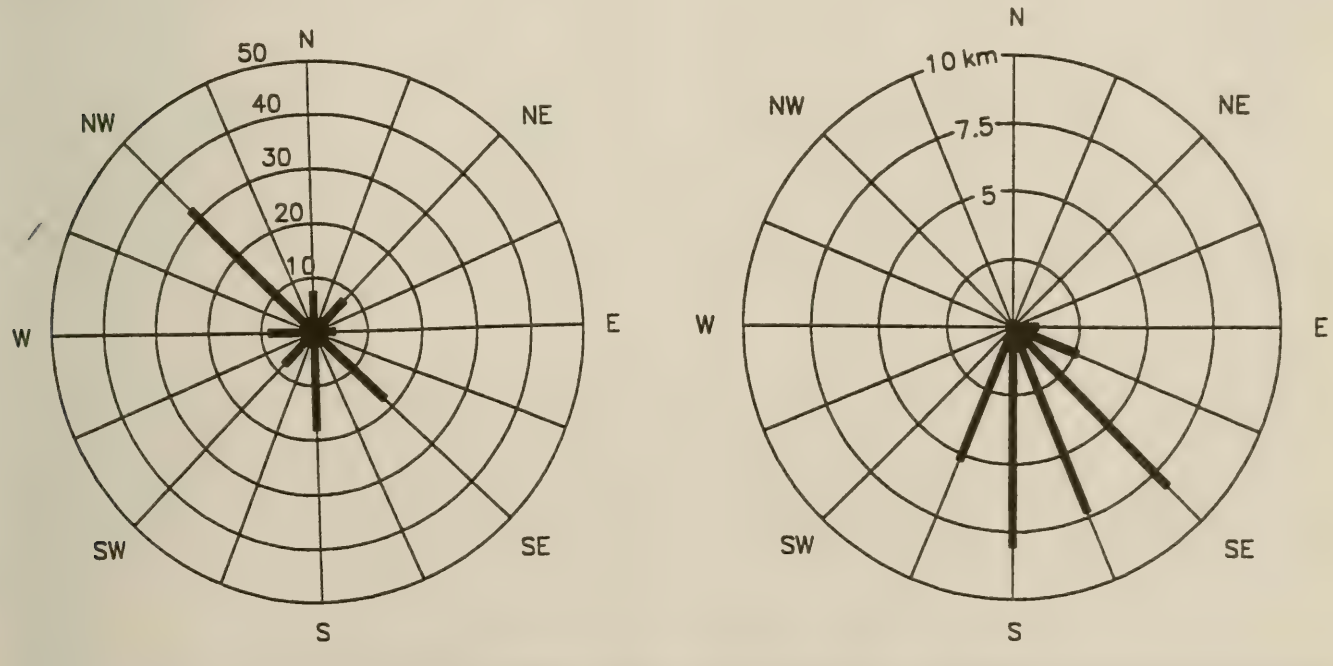

FIGURE 3. Average annual wind direction at Waskesiu Lake for the period 1977 to 1982 (left) and lake fetch for the northeast shore of Waskesiu Lake (right) [after Cote 1984].

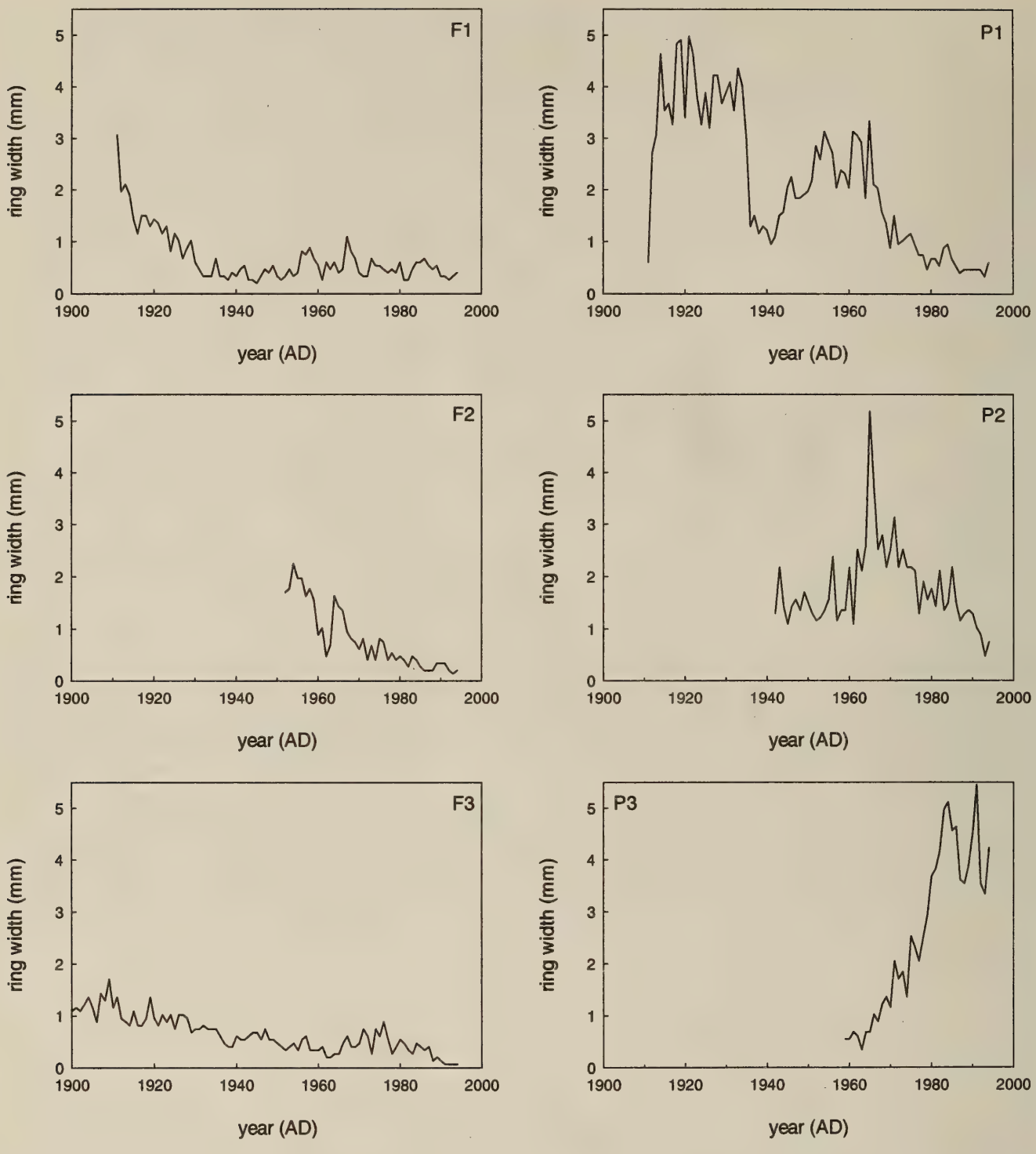

FIGURE 4. Annual tree ring widths for selected White Spruce ring trees growing in undisturbed forest and around the perimeter of slope failures.

Raspberry (*Rubus strigosus*) and Snowberry (*Symphoricarpos albus*) were represented at densities ranging from 0.8 to 4.6 individuals/m^2). The shrubs were most abundant in the lower part of the slumps with maximum density (12.1 individuals/m^2) occurring 10 m from the shoreline.

The trees at the base of the slumps were generally larger than those further upslope. Mean circumference for White Spruce ranged from 33.7 cm near the shoreline compared to 2.5 cm at the top of the scars. Similarly, mean circumference for Balsam Poplar decreased from 38.0 cm to 2.5 cm away from the shoreline. Some large White Birch and Trembling Aspen (> 60 cm circumference, age approximately 80 years) occurred on the scars and presumably survived the slumping events. Trees with stems typically less than 20 cm in circumference appeared to have established within the past 10 years. The older trees which were occasionally present at the base of some of the slumps typically exhibited marked curvature of the

trunk in response to slope instability. In some individuals the stems were bent near the top so that the lower trunk tended to grow perpendicular to the slope while the upper trunk had regained its vertical orientation. In other trees, the trunks were curved at the base which suggests that disturbance occurred when they were relatively young. The ages of the five White Spruce trees that were sampled ranged from 56 to 102 years: the curved part of the trunks developed 10, 15 and 21 years prior to felling which indicated slumping had occurred in 1973, 1979 and 1984.

Weather records and lake level data for Waskesiu Lake are incomplete. However, precipitation in 1973 and 1984 totaled 534 mm and 523 mm, respectively, which is well above the long-term normal of 398.9 mm. In 1978, one year prior to the 1979 slope disturbance, 526 mm was received (Figure 2). Similarly, the surface lake level in June 1973 was 532.6 m, the highest of any year in the 1970s, and in 1979 it was also high at 532.5 m. The configuration of the shoreline in this part of the lake provides a fetch of approximately 7.5 km to the south and southeast. This extent of open water coupled with the frequency of winds from this quadrant (Figure 3) could produce significant wave action along the base of the slopes Consequently, slumping in this environment is most likely triggered by high moisture contents of the surficial materials caused by subsurface seepage from the boggy area inland supplemented by wave action. Many of the tree seedlings found on the slumps exhibited bent stems caused by burial of the young tissue. This suggests that slope adjustment continues for several years following the initial slope failure. Such instability can be attributed to groundwater seepage, rain splash and the activity of ants, all of which were observed to dislodge the loosely consolidated mineral soil particles on these poorly vegetated slopes.

Characteristic ring width patterns for trees in undisturbed forest and those growing adjacent to the slumps are presented in Figure 4. The older forest trees (F1, Figure 4) typically exhibited curvilinear growth patterns in which the annual ring width gradually decreased with age. For this individual, early growth may have been stimulated by a tree fall gap, but average annual growth declined to less than 1 mm y^{-1} with subsequent canopy closure. Incremental growth rates for younger trees (F2, Figure 4) that have been suppressed by the overstory were typically about 0.5 mm y^{-1}. Many of the older trees growing along the perimeter of the slumps exhibit accelerated growth phases. For example, early growth rings for specimen P1 (Figure 4) exceeded 4 mm y^{-1} in some years, decreased sharply in the 1930s, and exceeded 3 mm y^{-1} in the 1950s and 1960s. The growth pattern suggests that the tree has survived periodic slumping. Initial establishment and rapid early growth probably coincides with a reduction in competition at the site while the period of depressed activity may reflect root disturbance associated with a subsequent slump. This tree survived and again benefited from the disturbance. A corresponding period of accelerated growth during the early 1960s can be seen in younger individuals (P2, Figure 4) growing along this active shoreline, while trees which established soon after these slumps occurred (P3, Figure 4) have grown more rapidly than their counterparts in the forest. Tree growth rates generally decline with age and there is a corresponding decrease in annual ring widths. However, in some forest trees (e.g. F3, Figure 4) increased growth was noted in the mid 1970s. This may be linked to higher than normal precipitation during this decade (Figure 2).

Conclusions

Slope failures along the northeastern shoreline of Waskesiu Lake can be identified by distinctive vegetation patterns. Recently disturbed slopes were characteristically colonized by a sparse cover of herbaceous plants and tree seedlings, and contrasted with the adjacent slopes which supported a mixed forest cover dominated by White Spruce, Balsam Fir and Paper Birch. On the slumps, 35 herb and grass species were found. Northern Bedstraw (*Galium borealie*) was the dominant species, followed by Horsetail (*Equisetum arvense*), Two-Leaved Solomon's Seal (*Maianthemum canadense*), American Vetch (*Vicia americana*) and Wild Sasaparilla (*Aralia nudicaulis*). The greatest density of herbs and grasses occurred near the base of the slumps, where soil moisture conditions were the most beneficial for plant growth.

Slumping is most likely caused by subsurface seepage, with annual fluctuations in lake level and seasonal wave activity possibly contributing to the process. Tree ring data indicated that slumping occurs periodically with the most recent events dated at 1973, 1979 and 1984. These years either received higher than normal precipitation or had above normal lake levels (Figure 2). As well as contributing to higher lake levels, wet years can also promote slope instability by increasing the water content of the surficial materials, thereby decreasing their shear strength. Statistical analysis indicated that there is no simple relationship between precipitation, temperature, lake level and the occurrence of slumping. The impact of slumping on the forest vegetation structure, however, is substantial. Consequently, lake level changes caused by changes in precipitation and temperature and by human activities such as the removal of the Kingsmere River weir in 1999 may initiate further changes in the shoreline forest vegetation.

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Rare and Endangered Fishes and Marine Mammals of Canada: COSEWIC Fish and Marine Mammal Subcommittee Status Reports: XIII

R. R. CAMPBELL

131 Dahlia Avenue, Ottawa, Ontario K1H 6G1, Canada

Campbell, R. R. *Editor*. 2001. Rare and endangered fish and marine mammals of Canada: COSEWIC Fish and Marine Mammal Subcommittee Status Reports: XIII. Canadian Field-Naturalist 115(1): 115–117.

Seven status reports representing the 1998 fish and marine mammal status assignments have been prepared for publication. Committee (COSEWIC) and Subcommittee (Fish and Marine Mammals) activities are briefly discussed.

Sept rapports de statut relatifs aux poissons et aux mammifères marins auxquels ont été attribués un statut en 1998 ont été préparés pour publication. Les activités du Comité (CSEMDC) et du sous-comité (des poissons et des mammifères marins) sont brièvement discutées.

Key Words: Rare and Endangered species, fish, marine mammals, COSEWIC.

As indicated in previous submissions (Campbell 1984 through 1998), the intent of the Subcommittee on Fish and Marine Mammals is to publish (as funding permits) the status reports (on those species of fish and marine mammals) which the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has reviewed, approved and used as a basis of assigning status to species in jeopardy in Canada. The group of reports presented here represent seven of the nine fish and marine mammals considered by COSEWIC which were assigned status in 1998 (*see* COSEWIC 1998). In addition, reports on the Redfin Pickerel (*Esox americanus americanus*) and the Atlantic Cod (*Gadus morhua*) were also considered (the former was found to be Not At Risk, and the latter Vulnerable), but revised manuscripts have not as yet been received from the authors. In the meantime, summaries of these (and any and all reports) are available from the COSEWIC Secretariat (Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3). It is hoped that we will be able to find continuing financial support to offer, in succeeding volumes, those reports reviewed in future years, as well as those not received in time for this publication.

Progress

COSEWIC has undertaken to make available to all Canadians supporting information on each species classified (*see* Cook and Muir 1984; Shank 1999). The Fish and Marine Mammal Subcommittee has been able to use this journal as one step in achieving the goal. A series of reports have appeared in various volumes and numbers from 1984 through 1998 [*see* Canadian Field-Naturalist 98(1): 63–133; 99(3): 404–450; 101(2): 165–309; 102(1): 81–176 and 102(2): 270–398; 103(2): 147–220; 104(1): 1-145; 105(2): 151–250; 106(1): 1–72; 107(4) 395–546; 110(3): 462–532; 111(2): 249–307; 112(1): 94–157].

As of April 1998, COSEWIC has reviewed the status of 97 fish species, two marine invertebrates, and 43 marine mammals (*see* COSEWIC 1998). Of the 155 species (or discrete populations) investigated eight are indeterminate (six fish, two marine mammals), 63 (29 fish, 33 marine mammals, one marine invertebrate) have been found not to require status designation and another 47 (41 fish, six marine mammals) have been designated as vulnerable, mainly due to natural rarity; leaving 27 species (18 fish, nine marine mammals) of immediate concern (threatened and endangered), and 10 species (six fish, three marine mammals, and one marine mollusc) extinct or extirpated.

As of April 1998 there are 50 status reports on fish species (includes 22 updates), one marine mollusc (update), and 11 on marine mammal species (six updates) under review or in preparation (Table 1; Campbell 1998: Table 1). Several of these were to be presented to the Committee for status assignment in 1999.

As well, some 73 additional species of fish (plus 21 to be updated), one marine mammal update, and 12 marine invertebrates have been identified as being worthy of consideration (Table 2; Campbell 1998: Table 2). A few may be found to not require status designation, but the process serves to bring together the information necessary to make the appropriate determination and satisfy the need to fill those knowledge gaps. Although some of these may be of no immediate concern, the Subcommittee will, as opportunity allows, attempt to document the status of these species to determine their status in Canada.

TABLE 1. New (since Campbell 1998: Table 1) fish and marine mammal species updates and reports which are in preparation or under review as of April 1998.

Species	Scientific Name	Proposed Status
FISH		
Morrison Creek Lamprey*	*Lampetra richardsoni*	Threatened
Aurora Trout°*	*Salvelinus fontinalis timagamiensis*	Endangered April 1987
Shortnose Cisco°	*Coregonus reighardi*	Threatened April 1985
Shortjaw Cisco°	*Coregonus zenithicus*	Threatened April 1987
Redside Dace°	*Clinsotomus elongatus*	Vulnerable April 1987
Silver Shiner°	*Notropis photogenis*	Vulnerable April 1987
Greater Redhorse	*Moxostoma valenciennesi*	Vulnerable
Hadley Lake Stickleback Species Pair*	*Gasterosteus* spp.	Extinct
Balkwell Lake Stickleback Species Pair*	*Gasterosteus* spp.	Endangered
Emily Lake Stickleback Species Pair*	*Gasterosteus* spp.	Endangered
Priest Lake Stickleback Species Pair*	*Gasterosteus* spp.	Endangered
MARINE MAMMALS		
Fin Whale°	*Balaenoptera physalus*	Vulnerable April 1987
Humpback Whale°	*Megaptera novaeangliae*	
Northwest Atlantic		Vulnerable April 1985
Northeast Pacific		Threatened April 1982
Harbour Porpoise	*Phocoena phonoeca*	
Northwest Atlantic°		Threatened April 1990
Northwest Atlantic°		Threatened April 1990

*Endemic to Canada
°Updated Status Report

In addition to soliciting further status reports on species of concern, the Subcommittee continues to obtain updates on the status of selected species as new information becomes available, or in the 10 year review process initiated in 1993 (Table 2; Campbell 1998: Table 2) for those species which had not already received further examination following the initial assignment of status.

TABLE 2. New (since Campbell 1998: Table 2) fish and marine mammal species of possible interest to COSEWIC. (not listed by priority).

Species	Scientific Name	Proposed Status
FISH		
Blackfin Cisco	*Coregonus nigripinnis*	Threatened April 1988
Kiyi	*Coregonus kiyi*	Vulnerable April 1988
Umatilla Dace	*Rhinichthys umatilla*	Vulnerable April 1988
Bigmouth Buffalo	*Ictiobus cyprinellus*	Vulnerable April 1989
Black Buffalo	*Ictiobus niger*	Vulnerable April 1989
Black Redhorse	*Moxostoma dusquesnei*	Threatened April 1988
Margined Madtom	*Noturus insignis*	Threatened April 1989
Redbreast Sunfish	*Lepomis auritus*	Vulnerable April 1989
Orangespotted Sunfish	*Lepomis humilis*	Vulnerable April 1989
Banded Killifish	*Fundulus diaphanus*	Vulnerable April 1989
Enos Lake Stickleback*	*Gasterosteus sp.*	Threatened April 1988
Fourhorn Sculpin	*Myoxocephalus quadricornis*	Vulnerable April 1989
Blackline Prickleback	*Acantholumpenus mackayi*	Vulnerable April 1989
Bering Wolffish	*Anarichus orientalis*	Vulnerable April 1989
MARINE MAMMALS		
Sowerby's Beaked Whale	*Mesoplodon bidens*	Vulnerable April 1989

*Endemic to Canada

Concluding Remarks

The seven reports included in the following series are reports on the status of the respective species in Canada. Status was assigned by consensus of the COSEWIC Committee based on these reports which are published under the name(s) of the original author(s). The reports have undergone minor editing to provide a brief introduction and some degree of consistency in format and presentation.

Acknowledgments

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Status of the White-Beaked Dolphin, *Lagenorhynchus albirostris*, in Canada†

JON LIEN[1], DAWN NELSON[2], and DONG JIN HAI[3]

[1]Whale Research Group, Memorial University of Newfoundland, St. John's, Newfoundland AlC 5S7, Canada
[2]College of the Atlantic, Bar Harbour, Maine, USA
[3]Institute of Oceanology, Academia Sinica, 7 Nan Hai Road, Qingdao, Shandong, China

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White-beaked Dolphins are common and abundant in the north Atlantic. Abundance appears greater in northeastern areas compared to the northwestern Atlantic where its range extends from Davis Strait to the Hague Line on George's Bank, and into U.S. waters. Relationships between populations observed in different areas are not known. Total or local populations are not known to be reduced or depleted. The biology and ecology of this species has been incompletely studied. It occurs in social groups ranging from dozens to hundreds of individuals; there is some indication that groups may segregate based on age/maturity. Sexual maturity occurs in females at lengths from 1.74 to 2.49 m; 50% are mature at 2.42 m. Males are larger at sexual maturity (2.5l to 2.57 m). Factors limiting northwestern Atlantic White-beaked Dolphins may include hunting, incidental entrapments in fishing gear, ice entrapments and, possibly, pollution. Such factors should be monitored carefully but are not, at present, believed to have substantial impacts on the species, although there may be reduction of some local populations. Factors such as ice entrapments, parasites, infections, mass strandings and predation are recognized as naturally occurring mortality and are not presumed to normally limit the species. There is no evidence of any major threat to this species in zones under Canadian jurisdiction. However, careful monitoring of hunting activities in Labrador is recommended and fisheries by-catches should be carefully monitored.

Key Words: Cetacea, Odontoceti, toothed whales, White-beaked Dolphin, Dauphin à nez blanc, *Lagenorhynchus albirostris*.

The White-beaked Dolphin, *Lagenorhynchus albirostris* Gray 1846 (Figure l), is one of two species of *Lagenorhynchus* found in the North Atlantic, the other being the Atlantic White-sided Dolphin, *Lagenorhynchus acutus*. On occasion, groups may contain both species (Haase 1987). *Lagenorhynchus albirostris* can be differentiated from the White-sided Dolphin by its more diffuse colouration, especially just behind the dorsal fin, and fewer teeth (Mercer 1973; Leatherwood et al. 1976; Reeves et al. 1996*). White-beaked Dolphins generally have a more northerly distribution than White-sided Dolphins.

In the literature *Lagenorhynchus albirostris* is, on occasion, called the Whitenose Dolphin (Amundin and Amundin 1975). Along the Labrador coast they are most commonly known locally as "jumpers" or "squidhounds", but are also inappropriately called "herring hogs". The latter name is more precisely applied to Minke Whales, *Balaenoptera acutorostrata* (Reeves et al. 1996*). The name "grampus" is frequently applied indiscriminately to all dolphin species, and to Minke Whales in some areas of Newfoundland and Labrador (Lien et al. 1985). Reeves et al. (1996*) gives common names for White-beaked Dolphins in European waters.

Although sightings of *Lagenorhynchus albirostris* have been reported as common, and it is often found stranded on both sides of the Atlantic, little is known about its biology or population ecology (Klinowska 1991). The species is commonly ice entrapped along the Newfoundland coast, occasionally caught incidentally in fishing gear (Dong et al. 1996; Lien 1988), and opportunistically hunted (Alling and Whitehead 1987; Brice-Bennet et al. 1977). The purpose of this paper is to review the current status of *Lagenorhynchus albirostris* in the northwest Atlantic in waters under Canadian jurisdiction.

Appearance

Lagenorhynchus albirostris (Figure l) is generally black or dark grey, with one patch of light grey behind the dark dorsal fin and another which extends along the side (Jonsgård 1962; Mercer 1973; Leatherwood et al 1976). The "white beak", from which the species derives its common name, can in fact be dark grey or mottled (Jonsgard 1962; Corbet and Southern 1977; Leatherwood and Reeves 1983). Anterior to the dorsal fin in some animals there is a grey chevron which can extend into an irregular strip along the animal's sides, and into the dorsal patch. The dorsal patch behind the dorsal fin may vary from white to shades of grey and is a useful field trait for distinguishing *Lagenorhynchus albirostris* from *Lagenorhynchus acutus*. The underside of White-beaked Dolphins is white; the flip-

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*See Documents Cited section.

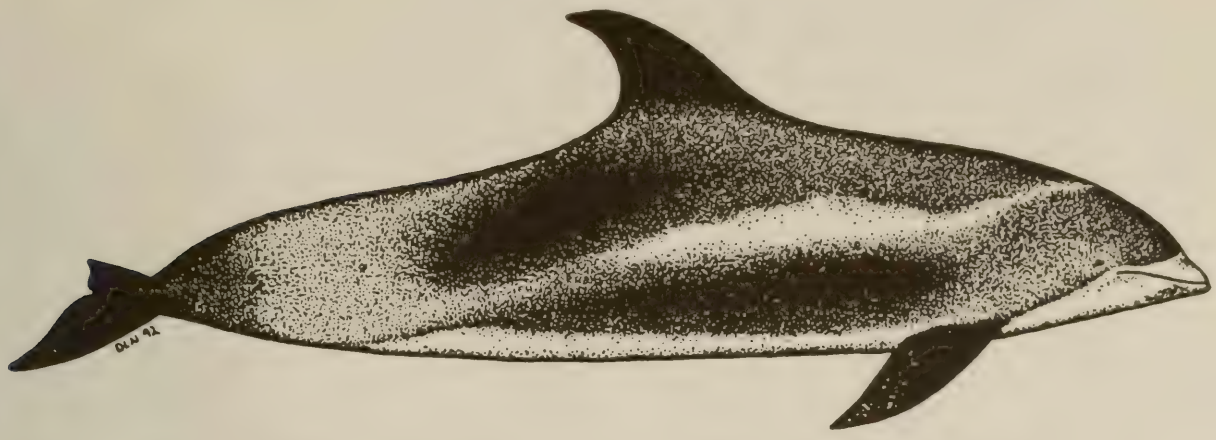

FIGURE 1. White-beaked dolphin (*Lagenorhynchus albirostris*). Drawn by Dawn Nelson.

pers and fluke are black. There is considerable variation in colouration among individuals (Reeves et al. 1996*), some of which may be attributable to age (Jonsgard 1962; Mercer 1973; Corbet and Southern 1977; DeBoer 1989).

Distribution

The White-beaked Dolphin is found only in cold temperate and subarctic waters of the north Atlantic (Leatherwood and Reeves 1983; Katona et al. 1993); it appears more common in eastern than western waters. In the northwest Atlantic (Figure 2), *Lagenorhynchus albirostris* occurs from eastern Greenland (Jonsgard 1962; Jonsgård and Christensen 1968; Christensen 1972; Benjaminsen et al. 1976), through the Davis Strait and south to Massachusetts (Mercer 1973; Leatherwood et al. 1976; Leatherwood and Reeves 1983; Boles 1980*; Winn and Edel 1980; Alling and Whitehead 1987). In the east, the species has been observed off Iceland (Mercer 1973; Andrésson 1978), the Norwegian Sea (Haug et al. 1981; Leatherwood and Reeves 1983; Øritsland et al. 1989), the Barents Sea (Christensen 1972; Benjaminsen et al. 1976; Leatherwood and Reeves 1983), occasionally in the Baltic Sea (Aguayo 1978; Leatherwood and Reeves 1983), and in the North Sea, including waters near Denmark, the Netherlands, England, and Scotland (Husson and Van Bree 1976; Corbet and Southern 1977; Evans 1980; Leatherwood and Reeves 1983; McBrearty et al. 1986; Baptist 1987; Smeenk 1989; Bakker and Smeenk 1990; Northridge et al. 1995). It is more rarely observed in the Irish sea (Evans 1980; Egan 1984; Jones 1984).

There is some evidence to suggest that *Lagenorhynchus albirostris* may be extending its range south in the eastern, but not in the western, Atlantic. Sightings south of 55 degrees latitude appear to have become more common in recent years. White-beaked Dolphins were first reported from France in 1981 and stranding records have continued since then (Collet and Duguy 1981; Duguy 1982, 1987). France appears to be the most southerly area frequented by this species as it has been reported only once from Portugal and not at all from Spain (Casinos and Vericad 1976).

Strandings are typically of single individuals. On the coasts of Britain and the Netherlands, strandings may have increased in recent years (Evans 1980). Bakker and Smeek (1990), studying records for the Dutch coast between 1900 and 1988, indicate that there may have been a slight increase in strandings during the 1960s. However, it is not possible to determine whether such fluctuations are actually trends in abundance, changes in distribution, or due to effort.

Protection

All whaling, except aboriginal, is prohibited in Canadian waters under the Marine Mammal Regulations of the Fisheries Act of 1867 (as amended to date). Some coastal Labrador residents might qualify for exemption to take White-beaked Dolphins but hunting there is conducted opportunistically without licences. In United States waters deliberate taking of cetaceans is prohibited by the Marine Mammal Protection Act of 1972. *Lagenorhynchus albirostris* is listed in Appendix II of CITES, and Appendix II of the Berne Convention (Klinowska 1991); such regulations would be applied to the import or export of live captures or tissues. The North and Baltic Seas populations are also included in Appendix II of the Bonn Convention (Klinowska 1991).

Population Size and Trends

Little is known about the actual abundance of this species. Although it is generally regarded as common, there is little substantive information on population sizes or trends. There is little study at present that could change this situation in the near future.

Western Atlantic. A survey, designed specifically for small cetaceans, was conducted in 1987 covering the 200 meter depth contour between St. Anthony,

FIGURE 2. Range (shaded area) of the White-beaked dolphin in the Northwest Atlantic.

Newfoundland, and Nain, Labrador. It resulted in an estimate of 3486 (C.I. 2001–4971) *Lagenorhynchus albirostris* (Alling and Whitehead 1987). Hay (1982), in earlier surveys primarily focused on large cetaceans in adjacent areas, also made estimates consistent with this population size. There are not other numerical estimates. White-beaked Dolphins appear off Labrador as ice recedes in June and occur in greatest abundance in August–September (Boles 1980*). Long-term historical trends in the utilization of this species for food, which could be related to northern coastal abundance, are not evident in Labrador (Brice-Bennet et al. 1977; MacKay and Orr 1987). Jonsgard and Christensen (1968) reported the species as common off southeast Greenland, while Leatherwood et al. (1976) indicated this species was more numerous in the northern portion of its western range.

There are no trends evident in sightings collected by the Lighthousekeepers Sighting Network (1979 to 1997) operated by Memorial University of Newfoundland (Lynch 1987; Lien, unpublished data). No trends exist in the incidental entrapments of White-beaked Dolphins in fishing gear in Newfoundland (Lien 1988; Lien, unpublished data). Sightings at Mt. Desert Rock in Maine are much less common now than they were prior to the late 1970s; they have also declined around Cape Cod during the same period (Katona et al. 1993).

Eastern Atlantic. In an aerial survey near Iceland Gunnlaugsson et al. (1988) recorded 942 White-beaked Dolphins which if extrapolated suggest a total population of at least a few thousand in Icelandic waters (Reeves et al. 1996*). Between 1974 and 1975, a total of 2500 to 3000 White-beaked Dolphins were sighted in the Barents Sea (Benjaminsen et al. 1976). Oien (1990) made a rough estimate of 132 000 (c.v. 0.266) dolphins, primarily White-beaked, in the Barents Sea based on sightings made during ship surveys. It should be noted that these surveys were designed for large cetaceans and may underestimate small cetaceans which were not the target of survey designs.

Although exact numbers are not known this species is also considered to be numerous in the North Sea with the greatest concentrations in the central and northern sectors (Brown 1975; Corbet and Southern 1977; Massey 1978; Evans 1980; Leatherwood and Reeves 1983; Bakker and Smeenk 1990; Reeves et al. 1996*). It has been reported as common near Sweden, northern Norway, Iceland, and around the Faroe Islands (Jonsgård 1962;

Mercer 1973; Aguayo 1978; Leatherwood and Reeves 1983).

It is difficult to estimate a population size given the local nature of most surveys and that they were primarily designed for other species existing data. The total population of White-beaked Dolphins in the north Atlantic has been estimated in the low hundreds of thousands (Reeves et al. 1996*).

Habitat

Generally White-beaked Dolphins are pelagic and found both on and off the coastal shelf. Specific habitat requirements for this species are unknown. Sightings are most common in nearshore waters of Newfoundland and Labrador but this may reflect the relatively greater effort which occurs there. They also occur on the Southeast Shoal (Whitehead and Glass 1985), an offshore area of the Grand Banks with nearshore habitat characteristics. Abundance is known to increase in Newfoundland and offshore with the presence of spawning Capelin, *Mallotus villosus*. The northward shift in abundance of *Lagenorhynchus albirostris* that occurs during summer months appears to follow the northward progression of spawning concentrations of Capelin (Carscadden et al. 1989). Capelin form spawning concentrations at fairly uniform temperatures (Shackell et al. 1994), however, sightings of White-beaked Dolphins around Newfoundland occur at all times of year in water temperatures from -1°C to + 15°C, in both winter and summer. Sightings of White-beaked Dolphins in December in the Barents sea near Svalbard occurred in association with concentrations of Capelin (J. Lien and I. Christensen, unpublished observations).

General Biology

Reproductive Capacity: Foetal lengths from pregnant females that died in an ice entrapment around Newfoundland in March ranged from 79 to 94 cm in length (Dong et al. 1996). Length at birth is reported to be 1.20 m, while maximum adult length and weight may be up to 3.10 m and over 305 kg respectively (Fraser 1974; Corbet and Southern 1977; Leatherwood and Reeves 1983; Perrin and Reilly 1984). Males are reported to be sexually mature at 2.50 to 2.60 m in length and females at 2.50 m (Perrin and Reilly 1984), however a pregnant female measuring 1.70 m in length has been observed (Dong et al. 1996). A sample from Newfoundland showed that male animals reach physical maturity, as indicated by completion of phalanges fusion, at a length of 2.80 m and an estimated age of 13 Growth layer Groups (GLGs), while most females become physically mature at a length of 2.60 m and an estimated age of 16 GLGs (Dong et al. 1996). Completion of phalanges fusion in the flippers was at 2.60 m (15 GLGs) in females and at 2.80 m (13 GLGs) in males (Dong et al. 1996).

In European waters about half of females reach maturity at 2.42 m (Reeves et al. 1996). The smallest sexually mature male was 2.51 m and the largest sexually immature male was 2.57 m (Reeves et al. 1996*). Evans (1980) suggested that the main breeding season of White-beaked Dolphins around Britain occurred between July and September based on the fact that all new-born and very young animals found stranded between 1913 and 1966 occurred between these months.

Movements: Migrations are poorly understood. White-beaked Dolphins are found in northern seas between spring and late autumn, although they appear to winter further south and some may remain there until the summer months (Leatherwood and Reeves 1983; Klinowska 1991).

In the northwestern Atlantic the Lighthousekeepers Sighting Network in Newfoundland report year round sightings of White-beaked Dolphins (Lien, unpublished data). Ice entrapments of this species on the northeast coast of Newfoundland occur from February to April (Dong et al. 1996). According to fishermen, this species is first seen off Labrador in late June, while the majority move north mainly in August (Alling and Whitehead 1987). The southern migration past Labrador apparently peaks in September (Alling and Whitehead 1987). Other sightings and strandings indicate that *Lagenorhynchus albirostris* are generally found along the Labrador coast in the summer months (Sergeant and Fisher 1957; Sergeant et al. 1970; Alling and Whitehead 1987). They have also been sighted on the Southeast Shoal of the Grand Banks in June and July, with numbers decreasing toward the end of this period (Whitehead and Glass 1985).

In the northeastern Atlantic strandings of White-beaked Dolphins on the Dutch coast are slightly lower in summer months (Bakker and Smeenk 1990). Sightings of White-sided Dolphins are common in British waters throughout the summer months, although the peak in sightings occurs between October and November for southwest England (Evans 1980). White-beaked Dolphins appear to be largely absent from the coastal waters of Britain between December and May (Evans 1980).

Feeding: White-beaked Dolphins are known to feed on Whiting (*Merlangius merlangius*), Bib (*Trisopterus luscus*), Poor-cod (*Trisopterus minutus*), Atlantic Cod (*Gadus morhua*), Herring (*Clupea harengus*), Haddock (*Melanogrammus aeglefinus*), squid, octopus, and sometimes benthic crustaceans (Sergeant and Fisher 1957; Corbet and Southern 1977; Evans 1980; Leatherwood and Reeves 1983; Smeenk 1986; Dong et al. 1996; Reeves et al. 1996*). Jonsgård and Christensen (1968) reported White-beaked Dolphins taking Capelin out of the mouths of feeding Fin Whales (*Balaenoptera physalus*). Stomach samples from ice entrapped animals on the southwest coast of

Newfoundland primarily contained Atlantic Cod, but some had remnants of crabs, *Chionoecetes opilio*, and seaweed; 20% of the stomachs contained fish hooks used on cod longlines (Dong et al. 1996). Ostrom et al. (1993) in a study of feeding in nine cetacean species found nitrogen isotope values, which are good indicators of the trophic level of feeding, that were consistent with a piscivorous diet in White-beaked Dolphins.

Social Behaviour: There is little information on social behaviours and social organization in *Lagenorhynchus albirostris*. White-beaked Dolphins can occur in large schools of several hundred, especially in the northeastern Atlantic (Corbet and Southern 1977; Evans 1980; Leatherwood and Reeves 1983; Haase 1987). Much smaller groups are typically encountered in the northwest Atlantic with reports of groups numbering 10 to 20 individuals being common (Sergeant and Fisher 1957; Amundin and Amundin 1975; Evans 1980; Anonymous 1983; Baptist 1987; Riddiford 1987; DeBoer 1989; Harvey 1990). Large schools may be associated with feeding or migration (Evans 1980).

Some groups are separated by age/maturity. Small groups have been observed to contain both adults and young (Evans 1980; Baptist 1987) although this is not always the case (Jonsgard 1962). Ice entrapped groups which have been examined in Newfoundland have been primarily composed young animals 1.89 to 2.41 m in length and an estimated 2 to 7 years of age. In such groups most animals were estimated to be 2 years of age; none were pregnant. Other groups were composed of large animals, estimated to be older than six years, with several pregnancies; other animals in this pod were very young animals estimated to me no more than one year of age (Dong et al. 1966).

In mass strandings, strong group cohesiveness can be displayed. Animals that are unbeached remain in areas where stranded animals are alive and vocalizing remain (Lien 1996).

Instances of bow riding by White-beaked Dolphins are common (Leatherwood et al. 1976; Jones 1984; Alling and Whitehead 1987; DeBoer 1989). Other behaviours observed in this species include high-speed travelling with shallow leaps, jumping and spinning on a longitudinal axis, high vertical leaps of up to five metres, and "foraging in a line" (Baptist 1987; Haase 1987).

White-beaked Dolphins sometimes associate with Common Dolphins (*Delphinus delphis*) (Haug et al. 1981; Jones 1984), White-sided Dolphins (Haase 1987; DeBoer 1989), Bottlenose Dolphins (*Tursiops truncatus*) (Evans 1980), and Fin Whales (Jonsgård and Christensen 1968). Humpbacks, *Megaptera novaeangliae*, have been observed tail slapping as groups of White-beaked Dolphins approach an area where the humpbacks were cooperatively feeding on capelin (Lien, unpublished observations).

White-beaked Dolphins produce several distinct types of sounds. Burst-pulses, presumably used for echolocation, had energy above 325 kHz with pulse rates from 100 to 750 pps and source levels over 200 dB re 1 UPa at 1 m (Mitson 1990). "Squeals", presumably used for social communication, range from 6.5 to 15 kHz (Schevill and Watkins 1962). These vocalizations are frequently produced by animals during confinement by ice entrapment or while stranded (J. Lien, unpublished observations).

Limiting Factors

A number of conditions could limit this species, but there is not firm evidence of significant impacts by any given factor.

Parasites: Nematodes, *Anisakis* spp., are the only parasites which have been reported in the stomachs of White-beaked Dolphins (Sergeant and Fisher 1957; Bratty and Clark 1992; Dong et al. 1996). Parasites are common in cetaceans generally and normally are not a serious limiting factor.

Infections: Buck and Spotte (1986) describe in detail the microbiology of several individuals of White-beaked Dolphins captured in Newfoundland during an ice entrapment and removed to a U.S. aquarium. All died from *Erysipelothrix rhusiopathiae* infections. Recent epidemic die-offs of dolphins in some areas due to viral infections, such as the morbillivirus (Duignan et al. 1996), could occur in White-beaked Dolphins.

In stranded animals, disease is common in the jaws and teeth (Harmer 1927; Fraser 1946; Van Bree 1977). In some stranded individuals teeth are missing (Reeves et al. 1996); in some instances, tooth loss may occur during process of beaching (Lien 1996*). Such dental deterioration could reflect aging.

Pollutants: Organochlorines and heavy metals have been documented in the tissues of white-beaked dolphins from the coast of Newfoundland (Muir et al. 1988) in amounts substantially higher than found in other cetacean species (Muir and Nordstrom 1993). A variety of contaminants, including PCB's and heptachlor epoxide have been found in animals from the North Sea (Kerkhoff et al. 1981; Law et al. 1991). There are few data available for species comparisons and "safe" levels of most pollutants are unknown.

White-beaked Dolphins in Newfoundland waters exhibited high values of contamination by DDTs and PCBs (4.5 to 89.0 ppm wet weight; and 4.7 to 182.0 ppm wet weight respectively)[Muir et al. 1988] compared to those found by Borrel (1983) in Faroe Island animals (0.57 to 29.3 ppm wet weight and 4.1 to 60.1 ppm wet weight respectively). These values compare with DDT accumulation in Beluga

Whales (*Delphinapterus leucas*) in the St. Lawrence Estuary of 1.16 to 225.6 ppm wet weight (Martineau et al. 1987) and PCBs from 0.22 to 576.0 ppm wet weight (Muir et al. 1990). Contaminants are believed to be having a detrimental effect on immune hormonal and reproductive functions in Beluga in the St. Lawrence Estuary population (Beland et al. 1991*; Martineau et al. 1994). There have been actions to prohibit and restrict point source discharges of PCBs. DDT use has been prohibited in Canada. This has reduced such introductions into the marine environment, but contamination persists by leachate from dump sites and recirculation of contaminants present in benthic sediments. Because of bioaccumulation of these compounds in White-beaked Dolphins levels will likely remain high and persist for some time. Monitoring of contamination levels should continue on a regular basis and stranded animals should be examined for medical impacts.

Incidental Entrapments in Fishing Gear: Incidental entrapments of White-beaked Dolphins in fishing gear are under-reported (Piatt and Nettleship 1987; Lien et al. 1988) and generally depend on obtaining log book or other data from the fishers themselves. Fishers have little motivation to report catches since entrapments of this species typically causes little gear damage (Leatherwood and Reeves 1983; Klinowska 1991; Lien et al. 1985; Dong et al. 1996). In some cases, incidentally caught individuals are used for human or animal food. Survey methods which require cooperation of fishers to accurately report catches may be seriously effected by the fishers views' of such by-catch and their assessment of its management implications (Lien et al. 1994). Because so little is know of the extent of incidental catches, the impact of by-catch on this species is almost completely unknown. As fisheries by-catch is known to effect other small cetaceans, such as the Harbour Porpoise, *Phocoena phocoena*, (Gaskin 1992), in northwestern Atlantic waters it should be carefully monitored.

Ice Entrapments: White-sided Dolphins regularly become caught in ice off the coast of Newfoundland during years of heavy pack ice (Sergeant and Fisher 1957; Muir et al. 1988; Dong et al. 1996). A total of 21 ice entrapments involving approximately 350 animals were reported in Newfoundland from 1979 to 1990; known mortality as a result of entrapment was about 55% (Dong et al. 1993). There have been fewer numbers of ice-entrapment events in more recent years (Lien, unpublished observations). Some animals that escape entrapments quite likely sustain injury and would likely show subsequent scars; some injuries may be serious and debilitating (Dong et al. 1996).

Mass Strandings: Mass strandings are less common in *Lagenorhynchus albirostris* than in *Lagenorhynchus acutus*. In Newfoundland there have been only three mass strandings from 1979 through 1996 (Dong et al. 1996; Lien 1996*) involving a total of 21 animals; mortality was 19%.

Predation: Reeves et al. (1996*) report Killer Whales (*Orcinus orca*) swimming with White-beaked Dolphins but are unsure if predation was occurring. Lien (unpublished observation) has observed tail slapping by Humpbacks as White-beaked Dolphins approached closely. This was presumed to be threat or aggressive behaviour, not predation; no injury or mortality was observed.

Hunting: Hunting of white-beaked Dolphins occurred historically in several areas of eastern Canada (Reeves et al. 1996. In more recent times hunting has been conducted opportunistically in several locations of Newfoundland and Labrador (Brice-Bennett et al. 1977; Mackey and Orr 1987; Sergeant and Fisher 1957; Alling and Whitehead 1987), Greenland (Heide-Jorgensen 1990), Iceland (Reeves et al. 1996*), Norway (Jonsgard 1962), and the Faroe Islands (Bloch and Joensen 1985). Generally hunting which now occurs in Canadian waters is opportunistic and in remote regions of Labrador where enforcement of regulations is minimal.

Numerical estimates of the extent of captures in a local population are given by Alling and Whitehead (1987) for southern Labrador. Here it was estimated, in 1982, that 10% of a population estimated to be 3486 individuals was killed, with an estimated 25 to 50 additional individuals struck but lost. Additional monitoring was done in the summers of 1985 and 1986 by interviewing Labrador fishers from L'Anse-au Clair to Cartwright (Lien, unpublished data) which found historical levels of catch near those estimated by Alling and Whitehead (1987), but estimated substantially under 100 animals for those years (1985 and 1986). In interviews, fishers frequently did not discriminate between Harbour Porpoise and several dolphin species; this tendency could seriously bias the numbers of White-beaked Dolphins estimated to be taken by hunting.

Special Significance of the Species

White-beaked Dolphins are a favourite species targeted by commercial whale-watching cruises in some areas. The White-beaked Dolphin is the toothed cetacean which is studied and used to introduce the Odontoceti, associated species and the ocean environment in school curricula in Newfoundland and Labrador. "Jumpers", including White-beaked Dolphins, are a dietary component in coastal peoples of Labrador (Alling and Whitehead 1987; Mckay and Orr 1984). Although the number of animals harvested for food is highly variable, the dietary importance of this hunt is thought to be reduced in recent years due to the availability of store-supplied foods. However, such hunting could impact local populations; additional monitoring is required.

Evaluation

Although White-beaked Dolphins are considered to be relatively common in the northwest Atlantic there are several factors potentially limiting populations including hunting, incidental entrapments in fishing gear, ice entrapments and possibly pollution. Such factors should be monitored carefully but are not, at present, believed to have substantial impacts on the species although there may be some reduction of local populations. Careful monitoring of hunting activities in Labrador is recommended. Factors such as parasites, infections, mass strandings, and predation are recognized as naturally occurring mortality and are not normally presumed to limit the species. Recent epidemics of disease in some dolphin populations may be exacerbated by anthropogenic conditions. Monitoring of fisheries by-catches is important as these removals impact local groups or the total population. There are no major threats identified for this species in the northwestern Atlantic in waters under Canadian jurisdiction.

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Updated Status of the Vancouver Island Lake Lamprey, *Lampetra macrostoma*, in Canada†

R. J. Beamish

Department of Fisheries and Oceans, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia V9R 5K6, Canada.

Beamish, R. J. 2001. Updated status of the Vancouver Island Lake Lamprey, *Lampetra macrostoma*, in Canada. Canadian Field-Naturalist 115(1): 127–130.

The Vancouver Lamprey was originally described in 1982 from a restricted area on Vancouver Island. It is a derivative of *Lampetra tridentata* (Pacific Lamprey), but has a larger disc and is able to survive and feed in freshwater. It feeds heavily on freshwater salmonids and juvenile anadromous Coho Salmon, *Oncorhynchus kisutch*, and would be a predator of other salmonids if it is introduced into other systems.

Key Words: Vancouver Island Lake Lamprey, Lamproie à grand disque, *Lampetra macrostoma*, parasitic lampreys, British Columbia, rare and endangered species, Petromyzontiformes.

The Vancouver Island Lake Lamprey, *Lampetra macrostoma*, (Figure 1) is endemic to Vancouver Island and is the only known *Lampetra tridentata*, Pacific Lamprey, derivative in Canada. It is also the only freshwater parasitic lamprey known from British Columbia. Originally described by Beamish (1982), the species was designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Vulnerable in 1986 (Beamish 1987).

Distribution

The Vancouver Island Lake Lamprey has been found only in two adjacent lakes, Cowichan Lake and Mesachie Lake, on Vancouver Island, British Columbia (Figure 3). Recently, two other populations of freshwater, parasitic *Lampetra tridentata* like lamprey have been reported from Village Bay Lake, Quadra Island and West Lake, Nelson Island, British Columbia (Figure 3), but their relationship with *Lampetra macrostoma* has not been studied. The larger lake is the 34 km long Cowichan Lake, which has a mean depth of 51 m and a maximum depth of 150 m. The much smaller lake, Mesachie Lake is 2 km to 7 km long and has a surface area of approximately 59 hectares and a generally uniform depth of 33 m.

Protection

There is no proposed protection or control for this species. If the distribution is confined to the two known lakes, then the species is rare. As local fishermen do not "like" this species, it may become endangered unless its importance as an isolated species is appreciated. It is also a potentially serious source of salmonid mortality, if introduced to other lakes.

The Conservation Data Centre ranks the species as G1, S1, ie., both globally and provincially critically imperiled and the Province (British Columbia) as "Red", i.e., threatened.

Population Size and Trend

No population estimates exist. The incidence of wounding and scarring on prey suggests that the population fluctuates. There is no indication that the population is in danger of extinction, but research on this species should be controlled. There has been no research since the mid-1980s. Further study is needed to identify biological and taxonomic relationships with its close relative the Pacific Lamprey and the two other reported *Lampetra tridentata* like specimens. There has been a recent decline in wild Coho, *Oncorhynchus kisutch*, (DFO 1998) and this may affect the survival or prey preference.

Habitat

The known distribution is extremely restricted. It is probable that its distribution results from anomalous patterns of glaciation during the last glacial period. There is no indication that habitat loss is reducing distribution, in fact, increasing siltation of lakes and rivers may be increasing habitat for ammocoetes. The species is a lake spawner and would be affected by loss of shallow water gravel areas used for spawning.

General Biology

Like all lake lampreys, the Vancouver Island Lake Lamprey reproduces only once. It is not possible to age an lamprey accurately, however, an "edu-

†Vulnerable status originally assigned by COSEWIC April 1986, reaffirmed April 1998.

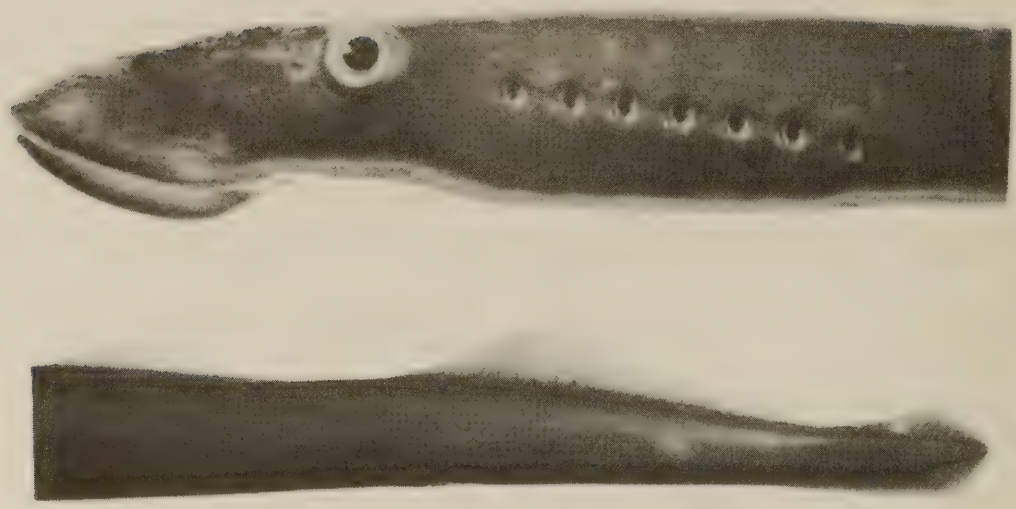

FIGURE 1. Head and tail regions of a 22.8 cm *Lampetra macrostoma* photographed live and captured in Lake Cowichan, November 1980.

cated guess" is that the species is about 8 years old when it reproduces (6 years as a larva and 2 years as a young adult and adult).

Lampreys appear to be able to increase in abundance relatively rapidly, indicating a relatively high rate of juvenile survival at low population levels. Also, lampreys are known to be at least 300 million years old, hence they are one of our most primitive and successful fishes. This indicates that this species and lamprey in general may be adaptable and capable of adjusting to a variety of pressures if allowed to behave naturally. However, this species is not found outside of the two lakes described and it is captured and killed by sport fishermen.

Thus, the biology of the Vancouver Island Lake Lamprey has not been well studied. It is known that spawning occurs from May to August, and during this period, there is an aggregation of males and females on the gravel based deltas. Spawning has been observed at the mouth of several creeks. Spawning areas varied from 20 cm to more than 2 m deep. Spawning occurred in the shallow water, but we could not determine if it occurred in water deeper than 15 cm. Larval lamprey are found in the lake in the vicinity of creeks and occasionally in the creeks, but always close to the lake. No Vancouver Island Lake Lamprey have been found more than a few hundred meters upstream of the lake in the few creeks that have been examined, and there were no lamprey in the creek connecting Mesachie Lake and Cowichan lake. This suggests that this species spawns in each lake and young remain in the lake. Spawning behaviour as observed in the laboratory is similar to the behaviour reported for *Lampetra richardsoni* and *Lampetra tridentata* by Pletcher (1963). It is only during the spawning period that adult lamprey are easily captured. Behaviour of young adults at other times is largely unknown and unstudied. Feeding juveniles have been caught by anglers when they have towed live fish on "stringers" behind their boat. While it is rare to land live lamprey in this manner, one fisherman landed three live Vancouver Island Lake Lamprey that had attached themselves to a live Cutthroat Trout (*Oncorhynchus clarki*).

The Vancouver Island Lake Lamprey metamorphoses into a young adult from July to October. From October to spring of the following year the young adult probably remains in the gravel. In spring, the young adult begins feeding and attacks large numbers of young salmonids, including age 1 and 2 Coho Salmon. Feeding juveniles readily attack resident fishes. Carl (1953) reported that 8 out of 10 fish examined from Cowichan Lake had evidence of lamprey attacks. Beamish (1982) observed that up to 50% of the salmonids captured in Mesachie Lake throughout the years had evidence of lamprey feeds without killing its hosts. Since salmonids remain in the lake and the lake is still popular for sport fishermen, it appears that the Vancouver Island Lake Lamprey coexists with its hosts in a manner similar to the landlocked Sea Lamprey, *Petromyzon marinus* in Cayuga Lake, New York, USA (Wigley 1959). Beamish (1982) reported that in one sample of 221 salmonids, 15% had wounds that penetrated deeply into the body

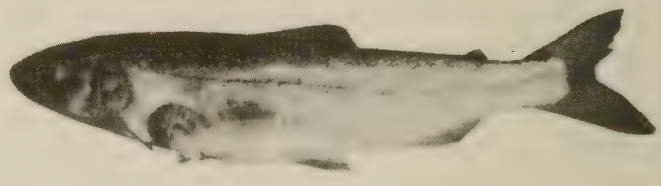

FIGURE 2. Coho showing fresh scar from a Lake Lamprey. The salmon was 19 cm in length and found dead on the bottom of Mesachie Lake. Notice the size of the scar relative to the size of the fish and the healed wound posterior to the fresh wound.

FIGURE 3. Distribution of the Vancouver Island Lake Lamprey, *Lampetra macrostoma*.

(Figure 3) and could cause mortality, thus some mortality does occur. The species feeds primarily on Coho Salmon and Cutthroat Trout. However, other salmonids such as Dolly Varden (*Salvelinus malma*) are attacked.

No Pacific Lamprey adults of ammocoetes have been found in the same area as the Vancouver Island Lake Lamprey. Pacific Lamprey do exist a few kilometers from the lake in the river flowing out of Cowichan Lake, but it is unknown if they occur in the lake. The timing and length of spawning period of the Vancouver Lamprey is different from the Pacific Lamprey that occur in the same area of British Columbia (Beamish 1980). The lake spawning habitat and the late spawning period could offer reproductive isolation from the Pacific Lamprey. It is important to note that this lamprey readily survives and feeds as a young adult in freshwater, whereas its close relative, the Pacific lamprey, cannot be kept as a young adult in freshwater (Beamish 1980; and unpublished data).

Limiting Factors

Unknown.

Special Significance of the Species

The Vancouver Island Lake Lamprey is endemic to Canada and is only known to exist on Vancouver Island. It is of considerable scientific interest, but it is unlikely that some sectors of the general public would understand or support its preservation and protection. Its occurrence in Cowichan Lake is of particular interest to the understanding of glacial history of Vancouver Island. Confirming the closest

relatives and the molecular genetic dating of the time it split off from a common ancestor would contribute to the study of glacial refugia on Vancouver Island. It is probable that this species will also provide important information about evolutionary processes in lampreys.

Evaluation

Comments from fishermen about the incidence of observed lamprey wounds suggest that the population fluctuates. Although no population estimates exist there has been no indication that there is a long term decline in numbers. There has not been an assessment of this species since the mid-1980s, but its restricted distribution indicates that it will probably remain confined to Cowichan Lake and Mesachie Lake. The abundance could be guessed to be between one or two thousand adults in both lakes. It is also possible that the recent decline in coho abundance has affected the survival or feeding habits, or both, but there have been no studies.

Acknowledgments

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Status of the Sympatric Smelt (Genus *Osmerus*) Populations of Lake Utopia, New Brunswick†

ERIC B. TAYLOR

Department of Zoology and Native Fish Research Group, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

Taylor, Eric B. 2001. Status of the sympatric smelt (genus *Osmerus*) populations of Lake Utopia, New Brunswick. Canadian Field-Naturalist 115(1): 131–137.

Lake Utopia, southwestern New Brunswick, contains phenotypically and genetically distinct populations of smelt, genus *Osmerus*. One form, "Dwarf Smelt", matures at between 100 to 120 mm total length, has 35 to 36 gill rakers, and spawns in small streams in May. The other form, " Normal Smelt", matures at 150 to 250 mm total length, has 30 to 32 gill rakers and spawns in larger, lake-headed streams in early April. The two forms are genetically distinct as assessed by differences in the frequencies of mitochondrial and nuclear DNA restriction fragment length polymorphisms. Quantitative genetic differences between the forms are suggested by inter-annually stable differences in morphology and spawning time and site. The two forms in Lake Utopia: (i) are reproductively isolated in sympatry and behave as distinct species, (ii) appear to have originated independently from sympatric forms in other lakes, and (iii) may have resulted from speciation within Lake Utopia. Both forms are subject to annual dip-net recreational fisheries. The Normal Smelt appears to be in no immediate danger, but Dwarf Smelt may be especially vulnerable owing to its apparently lower abundance and limited spawning distribution in small, easily disturbed streams.

Il y a deux populations d'Éperlan (genre *Osmerus*) dans le Lac Utopia dans le sud-ouest du Nouveau-Brunswick, qui peuvent être distinguées par leur génotype et leur phénotype. Le type "normal" atteint une longueur de 150 à 250 mm à maturité, possède 30 à 32 branchicténies et fraie au début avril, dans les ruisseaux qui aboutissent dans le lac. Le type nain atteint une longueur de 100 à 120 mm à maturitè, possède 35 à 36 branchicténies et fraie au mois de mai dans les petits cours d'eau. Les deux types se distinguent génétiquement par des différences dans la fréquence des fragments de restriction de l'ADN des mitochondries. La stabilité morphologique de chaque phénotype quant l'endroit et la période de frai suggèrent qu'il y aurait des différences génétiques quantitatives. Les deux types du Lac Utopia (i) sont isolés au point de vue reproductif en sympatrie et fonctionnent tel deux espèces, (ii) semblent avoir une origine indépendante des types en sympatrie dans les autres lacs, et (iii) pouraient être le résultat de spéciation dans ce lac. Les deux types sont pêchés au moyen d'épuisette chaque année, par des pêcheurs de loisir. Le type "normal" ne semble pas en danger immédiat, mais le type "nain" pourrait l'être car il paraît être moins abondant et ne fraie que dans quelques cours d'eaux qui sont facilement perturbés.

Key Words: Rainbow Smelt, *Osmerus*, speciation, Osmeridae, New Brunswick, parallel evolution.

The Rainbow Smelt, *Osmerus mordax* (Mitchill 1814), is a euryhaline osmerid fish native to watersheds tributary to the western North Atlantic Ocean from Long Island to Lake Melville on the Labrador coast (Scott and Scott 1988; Nellbring 1989). Throughout this native range, Rainbow Smelt may be anadromous, growing to maturity in nearshore marine environments before returning to freshwater streams to spawn in the spring, or they may reside permanently in freshwater. Like many north temperate freshwater fish, lake-dwelling Rainbow Smelt may exist as "dwarf-" or "normal-sized" individuals, maturing at 70 mm and 250 mm total length, respectively (Taylor and Bentzen 1993a). Dwarf smelt are usually morphologically specialized for plankton feeding while normal smelt appear to be macrophagous and are often piscivorous (see Taylor and Bentzen 1993a). There are at least five well-documented cases of lake populations consisting of sympatric dwarf- and normal-sized forms: Lac Heney, Québec; Green and Onawa lakes, Maine; Lochaber Lake, Nova Scotia; and Lake Utopia, New Brunswick (Lanteigne and McAllister 1983; Taylor and Bentzen 1993a). Sympatric forms differ in size-at-maturity, morphology, and feeding and reproductive ecology (Delisle 1969; Langteigne and McAllister 1983; Taylor and Bentzen 1993a).

Lanteigne and McAllister (1983) considered the dwarf form of *Osmerus* in northeastern North America to be a distinct species, the Pygmy Smelt (*Osmerus spectrum*) first described by Cope (1870) from specimens in Maine. Taylor and Bentzen (1993a), however, examined relationships among 19 anadromous, and dwarf- and normal-sized freshwater populations by assaying mitochondrial DNA (mtDNA) restriction site variation. The mtDNA data refuted the idea of monophyly of dwarf smelt and cast doubt on

†The dwarf form was assigned a Threatened status by COSEWIC, April 1998.

the validity of the designation *Osmerus spectrum*. There were no restriction sites that were diagnostic for dwarf or normal smelt, and dwarf-sized smelt populations did not cluster together and separately from normal-sized or anadromous populations. For instance, dwarf-sized smelt from Lake Utopia and Green Lake (previously diagnosed as *Osmerus spectrum*) as well as dwarf smelt from Lochaber and Onawa lakes were not monophyletic and were more similar to geographically proximate normal-sized or anadromous populations than to each other (Taylor and Benzten 1993a). Consequently, Taylor and Bentzen (1993a) concluded that dwarf *Osmerus* were polyphyletic and had diverged repeatedly, perhaps sympatrically, from geographically proximate normal or anadromous populations following deglaciation and that the various populations perhaps comprise a complex of undescribed biological species.

Although casting doubt on the validity of *Osmerus spectrum* as envisioned by Langteigne and McAllister (1983), the data of Taylor and Bentzen (1993a,b) established that in at least two lakes where they occurred sympatrically (Lake Utopia, New Brunswick and Lochaber Lake, Nova Scotia), dwarf and normal *Osmerus* were genetically distinct and, hence, reproductively isolated. Reproductive isolation in sympatry, coupled with interannually stable morphological and ecological differences between the forms (Figure 1) led Taylor and Bentzen (1993a,b) to conclude that dwarf and normal smelt in Lake Utopia fulfilled the criteria of distinct biological species (sensu Mayr 1963). Both forms in Lake Utopia, however, fall well within the morphological and molecular "boundaries" of *Osmerus mordax* relative to European Smelt (*Osmerus eperlanus*) and Arctic Rainbow Smelt (*Osmerus dentex*) (cf. Taylor and Dodson 1994) which complicates the taxonomic recognition of either or both of dwarf and normal smelt as distinct from *Osmerus mordax*. On average, however, the mtDNA data indicated that dwarf *Osmerus* from Lake Utopia were slightly more divergent from *Osmerus mordax* found outside Lake Utopia than were normal smelt (Taylor and Bentzen 1993a). Further, the divergence that has resulted in genetically distinct populations of dwarf and normal smelt in Lochaber Lake, Nova Scotia has occurred independently from that in Lake Utopia (Taylor and Bentzen 1993a). In all other lake systems where they co-exist, therefore, dwarf- and normal-sized smelt probably have arisen independently and the forms do not represent distinct lineages in northeastern North America (Taylor and Bentzen 1993a). Consequently, the status of dwarf and normal smelt from each lake where they are sympatric needs to be evaluated individually. As a first step in this process, this report summarizes what is known of the biology of the Lake Utopia smelt populations, outlines their scientific importance, and discusses issues relevant to their conservation.

Distribution

Lake Utopia (45° 10' N, 66° 47' W) is part of the Magaguadavic River drainage, Charlotte Co., south-

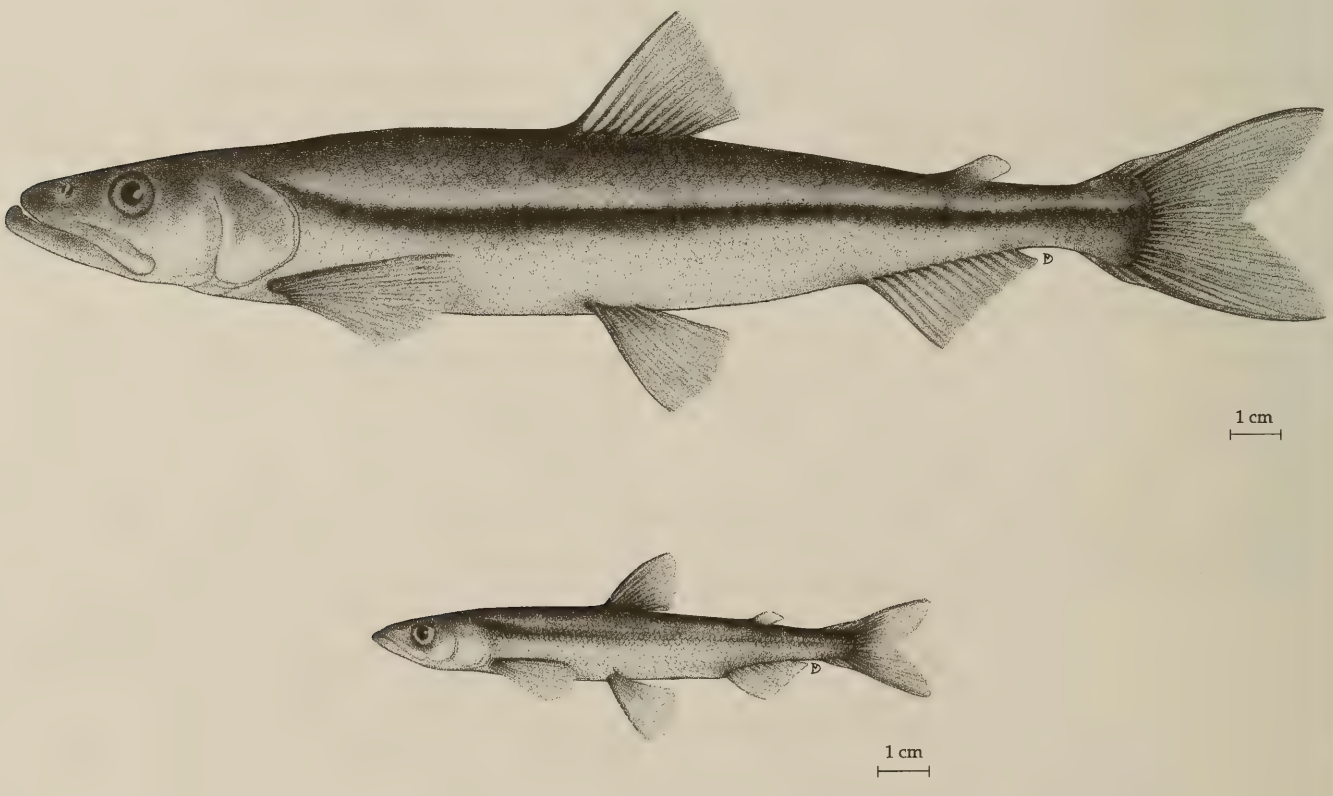

FIGURE 1. Illustration of Lake Utopia Normal (upper) and Dwarf (lower) Smelt (*Osmerus*). Both specimens were mature males.

western New Brunswick, and is located about 100 km SW of Saint John (Figure 2). Dwarf smelt from Lake Utopia were introduced into Meech Lake, Québec in 1924 (Dymond 1939) where they appear to have established a self-sustaining population because mature individuals have been collected as recently as 1991 (Delisle and Veilleux 1969; E. B. Taylor and N. Alfonso, unpublished data). Genetically distinct dwarf and normal smelt also occur in Lochaber Lake, Nova Scotia (Guysborough County) and these forms appear to have arisen independently from those in Lake Utopia (Taylor and Bentzen 1993a). Putative sympatric populations of dwarf and normal smelt (i.e., reproductive isolation between forms has not been confirmed by genetic means) also occur in Lac Heney, Gatineau River drainage, Gatineau Co., Québec (Delisle 1969); Green and Onawa lakes, Maine; Lake Champlain (Québec, Vermont, and New York); and Lake Kénogami, Québec (Delisle and Veilleux 1969). Current data indicates that sympatric smelt populations in northeastern North America have had independent origins (Taylor and Bentzen 1993a); the status of these other putative sympatric populations, therefore, will need to be evaluated independently from the Lake Utopia populations.

Protection

Exploitation of the smelt populations of Lake Utopia is limited to local dip-net fisheries during the spring spawning periods (April and May). Most of the effort appears to be focused on the Normal Smelt populations in Mill Lake Stream and Trout Lake Stream (Figure 2) owing to the ease of public access and larger spawning runs (E. B. Taylor, personal observations). Legal methods of fishing include gill nets, bag nets, box nets, dip-nets, and angling, but a closed season for the first three methods extends from 1 April through 14 October. Gill, box, and bag nets require a licence from the federal Department of Fisheries and Oceans, but none of these permits have been issued since the early 1960s (P. Cronin, New Brunswick Department of Natural Resources and Energy, R.R. 6, Fredericton, New Brunswick, personal communication). The dip-net fishery in Lake Utopia and its tributaries is open from 15 April to 31 May, with a daily catch and possession limit of 60 fish. There are no size limits in effect. Possession is permitted for domestic consumption only and ice fishing is not permitted on Lake Utopia (Anonymous 1996). A private Atlantic Salmon (*Salmo salar*) smolt farm is operated at the northeast end of the lake. Although the farm is land-based and freshwater-resident salmon are native to Lake Utopia (T. Vickers, N.B. Department of Natural Resources and Energy, personal communication), any accidental release of smolts into Lake Utopia could increase predation mortality on dwarf smelt and juveniles of both forms. A pulp and paper mill is also located near the southeast part of the lake, but its effluent does not enter Lake Utopia (Vickers, personal communication). Some protection of spawning streams is afforded indirectly by a game refuge at the northeast end of the lake that includes Mill Lake and its outlet stream.

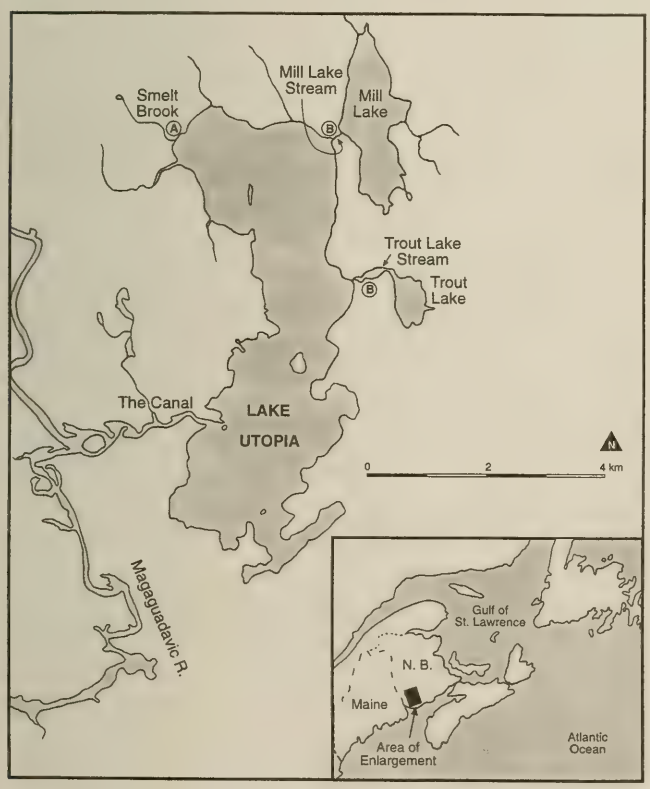

FIGURE 2. Lake Utopia and surrounding watershed including Dwarf ("A") and Normal Smelt ("B") spawning streams.

Population Size and Trends

No formal population census has been conducted in Lake Utopia for either dwarf or normal smelt. Personal observations by the author, however, over several nights during the spawning runs were made in 1991. Normal smelt in Mill Lake and Trout Lake streams appeared to number in the order of several thousand individuals. By contrast, numbers of dwarf smelt spawning in two streams at the northwest end of the lake appeared to be much less numerous; less than two hundred individuals were observed spawning over two nights. These observations are qualitative at best, but left the impression that in terms of maintaining viable smelt populations in Lake Utopia, dwarf smelt appear to be the form at greater risk. The exploitation of normal smelt in Lake Utopia in the annual spring dip net fishery is considered to be "low to moderate" (Vickers, personal communication). The extent of the dip-net fishery on dwarf smelt, however, is less well known owing, in part, to the relative remoteness of their spawning streams.

Habitat

Lake Utopia is a relatively shallow lake with average and maximum depths of 11.1 and 25.6 m,

respectively. The lake is 7.2 km long and covers an area of approximately 1370 hectares. The morpho-edaphic index is 0.94 and pH typically ranges from 7.0 at the surface to 6.4 at 25 m. The mid-summer (July) thermocline was at 10–15 m (27 August 1969) and temperatures ranging from 19°C (surface) to 7.8°C (25 m) were recorded on 3 July, 1969. The lake is frozen from early December until the first or second week in April (Vickers, personal communication).

Spawning habitat of dwarf and normal smelt from Lake Utopia appears to be largely confined to four small streams at head of the northern half of the lake (Figure 2). Normal smelt spawn in Mill Lake and Trout Lake streams, both of which are lake outlet streams. During spawning, these streams had high to moderate flows (up to 1 m/s) and are 2–5 m in width. Dwarf smelt spawned in two much smaller (1–2 m wide), slower-flowing streams (< 10 cm/s), both of which are not lake-headed. All of the land surrounding Lake Utopia or its tributary streams is privately-owned, and there is considerable cottage development, particularly in the south half of the lake.

General biology

Reproduction

Spawning normal smelt were collected in both Mill Lake Stream and Trout Lake Stream on 7 April 1980 at a water temperature of 4°C while Dwarf Smelt were collected from "Mill Brook" on 12 May 1980 (Lanteigne and McAllister 1983). Bridges and Delisle (1974) reported dwarf smelt spawning in Lake Utopia on 22 May 1972. Collections of dwarf and normal smelt made in 1990 and 1991 also indicated a large difference in spawning time between the forms; normal smelt were collected and observed to be ripe on 8–13 April 1991, whereas spawning dwarf smelt were collected on 7 May, 1990 and 10–12 May, 1991 (Taylor and Bentzen 1993b). Dwarf and normal smelt were both observed to enter the tributary streams at dusk with the greatest number ascending the streams and spawning between 21:00 and 04:00 (E. B. Taylor, personal observations). Interestingly, the smelt from Meech Lake that originated from a transplant of dwarf smelt from Lake Utopia were observed to spawn at the same time as the donor population: 8 May 1963 and 19 May 1971 (Bridges and Delisle 1974; Lanteigne and McAllister 1983).

Feeding Ecology

Dwarf smelt of Lake Utopia appear to be largely zooplanktivorous, Bajkov (1936) reported stomach contents to consist of *Diaptomous, Cyclops, Leptodora, Daphnia, Epischura,* and *Bosmina*. By contrast, normal smelt (at least once they surpass the average size of dwarf smelt) are macrophagous, often consuming juvenile smelt (presumably of both forms) (Bajkov 1936; E. B. Taylor, personal observation). Bajkov (1936) also reported that normal smelt may be taken by angling with artificial flies at the surface.

Size, Age, Growth, and Morphology

Dwarf and normal smelt collected from Lake Utopia in 1981 were reported to average (±SE) 96.9 (1.5) mm and 177.9 (4.1) mm in standard length, respectively (Lanteigne and McAllister 1983). Dwarf smelt collected in 1990 and 1991 averaged 142.9 (2.34) and 112.9 (1.84) mm total length, respectively (see Taylor and Bentzen 1993a). Normal smelt collected in 1991 averaged 226.0 (2.89) mm total length (Taylor and Benzten 1993a). There are no data concerning age or growth of the forms in Lake Utopia.

Morphological characterization of Lake Utopia dwarf and normal smelt was summarized by Taylor and Bentzen (1993a). In general, dwarf smelt have more gill rakers, larger eyes, but smaller mouths than normal smelt. The greatest differences are apparent in gill raker counts. Lanteigne and McAllister (1983) reported mean total gill raker counts of 34.1 (0.11) and 31.1 (0.30) in dwarf and normal smelt, respectively. Similar differences between the forms were reported by Taylor and Bentzen (1993a,b); gill raker counts for dwarf smelt collected in 1990 and 1991 averaged 36.2 (0.21) and 35.4 (0.20), respectively, and 32.8 (0.15) in normal smelt collected in 1991. Interannual stability of differences in gill raker counts between the forms is consistent with a genetic basis to trophic morphological differentiation between dwarf and normal smelt. Further, high gill raker counts of dwarf smelt are retained when fish are transplanted to different environments; total gill raker counts of Lake Utopia dwarf smelt collected in 1980 were not significantly different from those characterizing Meech Lake dwarf-sized fish (derived from Lake Utopia dwarf smelt) collected in 1963 (NMC71-0651, Copeman and McAllister 1978; Lanteigne and McAllister 1983).

Limiting factors

Production of Lake Utopia smelt is presumably regulated to some extent by the level of primary productivity of the lake. In addition, Lake Utopia contains populations of Atlantic Salmon and Brook Trout (*Salvelinus fontinalis*), both of which have been recorded to prey on smelt in Lake Utopia and elsewhere (Nellbring 1989; Sayers et al. 1989). Of five Brook Trout sampled from Lake Utopia during 1996, three were examined for stomach contents and all contained smelt. The Brook Trout ranged in size (TL) from 38.2 to 42.6 cm and the smelt ranged in size from 18.0 to 21.9 cm (Vickers, personal communication). The production of dwarf and normal smelt in Lake Utopia is potentially limited by predation pressure from salmonids, particularly on smaller sized juveniles and dwarf smelt. Furthermore, large smelt are often piscivorous and may include smaller smelt in their diet (E. B. Taylor, personal observations). It

is likely that a balance exists between smelt and their predators which may be a factor limiting smelt production in Lake Utopia. It is also possible that salmonid enhancement efforts in the lake could upset this balance and have negative impacts on production of juvenile stages of both forms and adult dwarf smelt. At present, enhancement of Lake Utopia salmonids is very limited; every other year Atlantic Salmon are planted into the lake at 1 fish for every 2 ha of lake surface area (Vickers, personal communication).

Perhaps the most important factor limiting smelt populations in Lake Utopia is the size and number of spawning streams. Although precise data are not available, the majority of spawning by normal smelt occurs in two streams at the northeast end of the lake (Figure 2) while dwarf smelt appear largely restricted to two much smaller streams at the northwest end of the lake. Although Trout Lake and Mill Lake streams are lake-headed and appear relatively stable in terms of long term persistence, the dwarf smelt spawning streams appeared to be more ephemeral and susceptable to habitat degradation owing to their small size.

Special Significance of the Sympatric Smelt

The significance of the Lake Utopia smelt populations comprises at least two areas concerned with the recognition of biological diversity. First, Lake Utopia smelt are part of a general phenomenon characteristic of many north temperate freshwater fish faunas where genetically distinct and reproductively isolated populations are sympatric and differentiated in morphological and ecological traits (e.g., Svardson 1961; McPhail 1984, 1992; Hindar et al. 1986; Foote et al. 1989; Verspoor and Cole 1989; Bernatchez and Dodson 1990; Ferguson and Taggart 1991; Taylor et al. 1996; Taylor et al. 1997). Because the forms are reproductively isolated and ecologically distinct in sympatry, Taylor and Bentzen (1993a,b) argued that dwarf and normal smelt in Lake Utopia fulfilled the criteria for recognition as biological species (*sensu* Mayr 1963).

The understanding of processes involved in speciation, the splitting of a single lineage into two or more reproductively isolated lineages, is a central theme of evolutionary biology. Such understanding is difficult to obtain directly because while one can observe the products of speciation (the species themselves), the processes involved are historical and, thus, impossible to observe. Notwithstanding this limitation, the principal model of speciation envisions genetic divergence during long term geographic partitioning of a lineage; i.e., allopatry. By contrast, the Lake Utopia smelt populations provide strong evidence of reproductive isolation developing postglacially (e.g. < 12 000 years — see Hughes et al. 1985) and in the absence of obvious geographic separation (Taylor and Bentzen 1993a,b). The data and arguments in favour of such relatively rapid, sympatric divergence in Lake Utopia have contributed to an increased appreciation of sympatric speciation as a legitimate and perhaps common mechanism of speciation (Bush 1994). The argument that sympatric speciation, while possible, is a "minor" or "rare" mechanism relative to allopatric speciation (see Gibbons 1996, page 1499), simply heightens the importance of the Lake Utopia populations where sympatric divergence has been postulated to occur. Some perspective of the scientific importance of the Lake Utopia smelt can be gained by appreciating that similar evidence for sympatric divergence put forth for Lake Utopia smelt has also been suggested to explain the explosive speciation of cichlid "species flocks" in Great Rift and crater lakes of Africa (Meyer et al. 1990; Schliewen et al. 1994). Further, because the divergence of Lake Utopia smelt populations appears to have occurred independently of divergence between smelt populations in other lakes (see Taylor and Bentzen 1993a) they provide an example of parallel evolution and the possible importance of deterministic processes, such a natural selection, in speciation (Schluter 1996).

Second, dwarf and normal smelt in Lake Utopia are, at present, not distinguished from one another taxonomically and such designations are not necessarily a simple matter (see discussion by Taylor and Bentzen 1993b). The uncertainty concerning their taxonomic recognition, however, cannot obscure the reality of their evolutionary and ecological distinctions and illustrates that considerable biodiversity is "hidden" and taxonomically unrecognized, and perhaps is unrecognizable using our current system of latin binomials (Taylor 1999). Situations such as the smelt of Lake Utopia, therefore, present a challenge to conservation philosophies and programmes focused on current taxonomic procedures.

Evaluation

The smelt populations in Lake Utopia are apparently stable and in no immediate danger. The major spawning streams of the normal smelt are located in a game reserve and fishing pressure appears not to be excessive. A major data limitation relevant to their evaluation is the lack of information on the population trends, spawning habitat area and protection, and fishing pressure on the dwarf smelt. As with many other fishes, one of the greatest potential dangers facing the smelt populations are introductions of exotic species (e.g., Allendorf 1991) or enhancement of native game fish which are predators of smelt. Artificial increases in Atlantic Salmon or Brook Trout in the lake could upset any predator-prey equilibrium that may exist in the lake and may be particularly important for the dwarf smelt which are within the size range of salmonid prey for throughout their life.

Acknowledgments

My interest in Lake Utopia smelt populations was stimulated by discussions with D. M. Blouw and D. E. McAllister. I have greatly appreciated the many helpful discussions concerning the evolution of Lake Utopia's smelt populations that I have had with J. D. McPhail and D. Schluter. P. Cronin and T. Vickers (New Brunswick Department of Natural Resources and Energy) provided advice and information concerning the biology and exploitation of Lake Utopia smelt. I appreciate comments made on an earlier version of this report by J. S. Nelson, E. J. Crossman, and A. Dextrase. The illustrations of smelt (Figure 1) were made by D. McPhail and were facilitated by the generous loan of specimens by D. McAlpine of the New Brunswick Museum (Natural History Division). Partial funding for this report was provided by NSERC operating grant 586196 awarded to EBT and by COSEWIC.

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Updated Status of the Northern Madtom, *Noturus stigmosus*, in Canada†

ERLING HOLM[2] and NICHOLAS E. MANDRAK[3]

[2]Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario M5S 2C6, Canada
[3]Youngstown State University, Youngstown, Ohio 44555 USA

Holm, Erling, and Nicholas E. Mandrak. 2001. Updated status of the Northern Madtom, *Noturus stigmosus*, in Canada. Canadian Field-Naturalist 115(1): 138–144.

The Northern Madtom, *Noturus stigmosus*, is a small member of the family Ictaluridae. It is disjunctly distributed in the Mississippi River and western Lake Erie drainage basins and has only recently been collected in Canada. There was insufficient information to assign a status in the original status report on the Northern Madtom. Recent collections indicate that reproducing populations are present in the Canadian waters of Lake St. Clair, the Detroit River and the Thames River. However, the stability, size and range of the populations are unknown; therefore, it is recommended that the Northern Madtom be classified as Vulnerable in Canada.

Key Words: Northern Madtom, chat-fou du nord, *Noturus stigmosus*, Vulnerable, Detroit River, Lake St. Clair, Thames River.

FIGURE 1. Northern Madtom, *Noturus stigmosus* Taylor, 1969, 77 mm TL, Detroit River. © 1996, Joseph R. Tomelleri.

The Northern Madtom, *Noturus stigmosus* Taylor 1969, (Figure 1) is one of 25 species in the genus *Noturus* of the bullhead catfish family Ictaluridae (Robins et al. 1991). Only one specimen was known from Canada at the time the original status report was written (Goodchild 1993); therefore no status was assigned.

Species in the genus *Noturus* can be distinguished from other genera in Ictaluridae by an adipose fin that is a long, low, ridge-like extension of the caudal fin (Scott and Crossman 1973; Page and Burr 1991). However, in the Northern Madtom, the adipose fin appears to be almost completely separated from the caudal fin by a deep notch.

The Northern Madtom has an overall colour pattern that is mottled with three irregular dark saddles on the back located at the front of the dorsal fin, behind the dorsal fin and at the adipose fin. Unlike the Brindled Madtom, *Noturus miurus*, the dorsal and adipose fins have pale distal margins. There are three or four irregular crescent-shaped bars on the caudal fin; the middle bar usually extending across the upper and lower caudal rays and touching the caudal peduncle. Two pale spots about three-

†Indeterminate status assigned by COSEWIC April 1993, reassessed April 1998 and Vulnerable status assigned.

quarters the diameter of the eye are usually present just anterior to the dorsal fin. Maximum total length is 132 mm. In spawning males, the head flattens, dark pigment diffuses and conspicuous swellings develop behind the eyes, on the nape, and on the lips and cheeks. This description is a compilation of diagnostic characters based on observations of ROM specimens and on those given by Page and Burr (1991), Etnier and Starnes (1993), and Trautman (1981).

Only five species of *Noturus* have been collected in Canadian waters (Coad 1995). One of these, the Margined Madtom (*Noturus insignis*), is likely not native to Canada (Mandrak and Crossman 1992) although some (McAllister and Coad 1974, Goodchild 1993) have suggested that it may be indigenous. *Noturus miurus*, and *Noturus stigmosus* differ from *Noturus insignis*, *Noturus flavus*, and *Noturus gyrinus*, in having a mottled pattern with saddles on the back instead of a more uniform brown or gray colour. The two mottled madtoms also differ from the plain-coloured madtoms in having the posterior edge of the pectoral spine strongly serrated instead of weakly serrated. Scott and Crossman (1973) indicated that specimens of *Noturus stigmosus* are very similar to *Noturus miurus* and should be watched for in collections from southwestern Ontario. The characters above distinguish *Noturus stigmosus* from *Noturus miurus* which has a dark blotch at the tip of the dorsal fin and a dark bar which extends to the extreme upper edge of the adipose fin. All specimens labelled *Noturus miurus* (40) in the fish collection of the Royal Ontario Museum (ROM) were examined and none were *Noturus stigmosus*. None of the *Noturus miurus* specimens in the Canadian Museum of Nature appear to be *Noturus stigmosus* (Goodchild 1993).

Prior to 1969 the Northern Madtom was considered a synonym of the Carolina Madtom, *Noturus furiosus*. Taylor (1969) described *Noturus stigmosus* as a distinct species and included it in the subgenus *Rabida* in the "*furiosus*-group" which included three other species of *Noturus* (*Noturus munitus, Noturus furiosus,* and *Noturus placidus*). He suggested that it was most closely related to *Noturus munitus*. Recent analysis of morphological, allozymic, and chromosomal data corroborates a monophyletic relationship among members of an expanded "*furiosus*-group" consisting of seven species (*Noturus furiosus, Noturus munitus, Noturus placidus, Noturus stigmosus, Noturus eleutherus, Noturus flavater,* and *Noturus flavipinnis*). Relationships within the "*furiosus*-group" are not clear and depend on the charac-

FIGURE 2. The North American distribution of Northern Madtom. Adapted from Rohde (1980) and Page and Burr (1991).

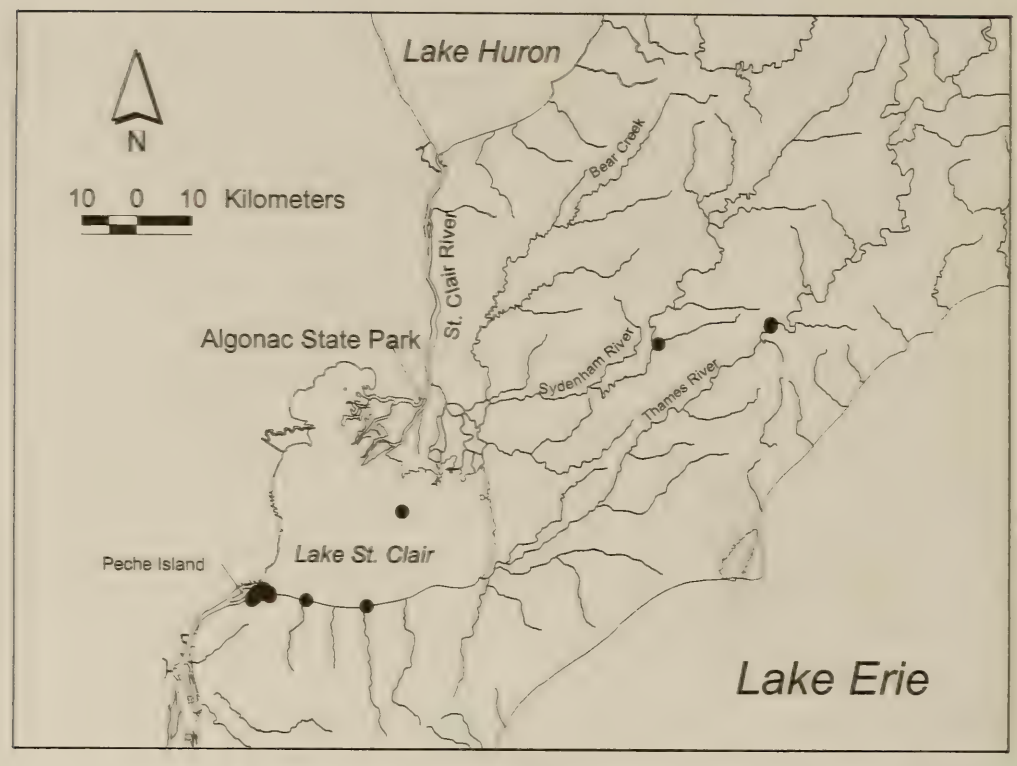

FIGURE 3. Canadian distribution of the Northern Madtom 1963–1999.

ters analyzed and the method of analysis (Grady and Legrande 1992). No subspecies of *Noturus stigmosus* have been recognized, but Mayden et al.(1992) indicated that it might be polytypic which may warrant its division into several species.

Distribution

The Northern Madtom is found in the Mississippi and western Lake Erie and Lake St. Clair basins (Figure 2). In the Mississippi drainage, it is found in several tributaries in Mississippi and Tennessee, in the main stem between Arkansas and Tennessee and throughout most of the Ohio River basin in Kentucky, Indiana, Ohio and restricted areas of Illinois, Pennsylvania and West Virginia. It is found in several western Lake Erie tributaries in Indiana, Michigan and Ohio; and, in the St. Clair River, Lake St. Clair and the Detroit River which form the border between Michigan and Ontario (Rohde 1980; Stauffer et al. 1982; Cincotta et al. 1986).

In Canada, the Northern Madtom is known only from the Detroit River, Lake St. Clair, and two tributaries of Lake St. Clair, the Thames River are the Sydenham River (Figure 3). The Northern Madtom has been known from the American side of the Detroit River since 1903 (University of Michigan Museum of Zoology; UMMZ 132009). It was first recorded in Canada in Lake St. Clair near the origin of the Detroit River where a single specimen was collected in 1963 (Trautman 1981). Another specimen was collected in 1994 near the first capture site on the Canadian side of the Detroit River (ROM 68328). In 1996, approximately 50 specimens were either captured or observed in the area around Peche Island. Also, in 1996, three juveniles were seined at night in Lake St. Clair at the mouth of Belle River approximately 19 kilometres east of the Detroit River.

The lack of Canadian records in the Detroit River and Lake St. Clair between 1963 and 1994 is likely the result of limited trawling and night seining, and incorrect field identification. Specimens captured in 1963 and in 1996 were collected primarily by trawling, a collecting method not commonly used on the Canadian side of Lake St. Clair and the Detroit River (Don MacLennan, Ontario Ministry of Natural Resources (OMNR), Lake St. Clair Fisheries Management Unit, personal communication). If previously collected, specimens might have been incorrectly identified since the Northern Madtom is not included in taxonomic keys commonly used in Canada (e.g., Scott and Crossman 1973).

In July 1991, an adult specimen was captured by the ROM in the Thames River near Wardsville. A juvenile specimen, captured in August 1997 at the site of capture of the adult, indicates that Northern Madtoms are established in the Thames River. Both specimens were captured by seining in the daytime in the direction of the current during periods when the water level was low enough to wade across the river. These records are approximately 90 kilometers from the nearest Lake St. Clair record at Belle River. There are no apparent barriers such as dams to prevent its dispersal from Lake St. Clair to the Thames River at Wardsville.

It has been recently recorded and is apparently established on the Michigan side of the lower St. Clair River at Algonac State Park (see Figure 3) (D. Jude, University of Michigan, personal communication). It is likely that this population dispersed there from the Detroit River via Lake St. Clair. Sampling by the ROM in 1996 (day and night trawls in 2-10 metres, and day and night seining in 0.1-1.3 metres) failed to capture it on the Canadian side of the St. Clair River. In 1999, a specimen was captured by a commercial fisherman in Lake St. Clair off Walpole Island (ROM 720938).

Protection

No specific legal protection exists for the Northern Madtom in Canada. The original COSEWIC report on the Northern Madtom concluded that insufficient scientific information was available to assign a status designation (Goodchild 1993).

The species and/or its habitat may be protected by the Canada Environmental Assessment Act, Canada Environmental Protection Act, Canada Fisheries Act, Canada Water Act, Canada Wildlife Act, Ontario Environmental Protection Act, Ontario Environmental Assessment Act, Ontario Game and Fish Act, Ontario Planning Act and Ontario Water Resources Act. A recent Natural Heritage Policy Statement, 2.3, of the Ontario Planning Act reduces protection for species classified as Vulnerable. Only habitats of Threatened and Endangered species are protected against development and site alteration (Ian Buchanan, Ministry of Natural Resources, personal communication).

The population of Northern Madtom in the Detroit River is in one of 43 "Areas of Concern". The Detroit River has been identified by the United States and Canada as having several beneficial uses which have become impaired. These include degraded fish and wildlife populations and loss of fish and wildlife habitats (Hartig et al. 1996). A Remedial Action Plan has been initiated and, if fully implemented, is likely to improve water quality, increase amount of fish habitat, and improve prospects for the survival of the Northern Madtom.

The Northern Madtom is listed as of Special Concern in the United States by Mayden et al. (1992). Johnson (1987) listed it as legally protected in Michigan and Ohio and as of Special Concern in Kentucky, Mississippi and West Virginia. It is listed as of Special Concern in Tennessee by Etnier and Starnes (1993). It was listed as Threatened in Kentucky by the Kentucky Nature Protection Commission, but Burr and Warren (1986) recommended downlisting it to Special Concern.

Global and North American federal, state and provincial conservation status and ranks were obtained from the Eastern Regional Office of the Nature Conservancy, Boston, dated 9 June 1997. The ranks assigned to Northern Madtom indicate that it is rare to extremely rare throughout its range:
Global Rank: G3
National Ranks: US: N3 Canada: N1
Regional Ranks: IL (SH-historic), IN(S1), KY (S1), MI (S1), MS (S3?), OH (S1S2), PA (S1), TN (S3), WV (S1), ON(S1)
1=extremely rare, 2=very rare, 3=rare to uncommon, 4=common, 5=very common

Population Size and Trends

No studies examining population size and trends have been conducted on the Canadian populations of the Northern Madtom. Recent collections of the species in Canada (37 specimens from 14 sites) and observations of males guarding larvae (MacInnis 1998) indicate that sustainable reproducing populations are established in the Detroit River, Lake St. Clair and the Thames River. The new records, including those from the St. Clair River on the American side, suggest that the species is undergoing a range expansion. However, these new records result from a more intensive sampling program of trawling and night seining specifically targetting the Northern Madtom. Therefore, it is uncertain that the population size is increasing. The Northern Madtom has not been captured in the Sydenham River since 1975 (NMC 75-1623) despite several sampling attempts in the 1990s. It is possible that it no longer occurs there.

Habitat

The preferred habitat of the Northern Madtom is clear to turbid water of large creeks to big rivers with moderate to swift current. It occurs on bottoms of sand, gravel and rocks occasionally with silt, detritus, and accumulated debris, and is sometimes associated with macrophytes (Taylor 1969; Smith 1979; Trautman 1981; Cooper 1983; Burr and Warren 1986; Robison and Buchanan 1988). In Ontario, it was trawled in the Detroit River at depths of 1-3m on smooth, firm bottoms often covered by macrophytes such as *Chara*. The surface waters were not turbid, but a gradient of increasing turbidity with increasing depth is present in the Detroit River (B. Ray, University of Windsor, personal communication). The Northern Madtom has also been seined at night in Lake St. Clair near the outlet of the Detroit River and around Belle River on sandy substrate devoid of cover. Two specimens were seined in the highly turbid Thames River (secchi < 0.2m) on a bottom consisting of sand, gravel and rubble from areas where the substrate was free from silt and clay. Current was moderate, maximum depth of capture was 1.2 m, water temperature was 23-26°C, conductivity was 666 μS, and pH was 7.9. In the St. Clair River, it has been collected in trawls at depths of 3-7 metres (D. Jude, University of Michigan, unpublished data).

Biology

Reproductive Capability

Nests are made under large rocks and in anthropogenic debris such as large submerged cans, milk bottles, and boxes. In Michigan, *Noturus stigmosus* reproduced slightly earlier than *Noturus miurus*, and clutch sizes were larger ranging from 61 to 141 eggs (Taylor 1969).

MacInnis (1998) observed and video-taped nesting of 21 adult Northern Madtoms in Lake St. Clair during the summer of 1996 while conducting research on the Round Goby, *Neogobius melanostomus*. Gravid females and recently spawned eggs were observed on 24 July 1996 in artificial goby nests set near Peche Island (see Figure 3). The nests were set in gentle current on a sandy bottom surrounded by a thick bed of aquatic macrophytes (primarily *Chara*). Eggs were approximately 3 mm in diameter and clutch size was conservatively estimated to range from 32 to 160. The male guarded both the eggs and newly hatched fry and, did not abandon the nest when disturbed. Larvae and juveniles about 9 mm total length were observed being guarded by males on 13 August. The temperature during this period was 23°C. A male Brindled Madtom was also observed nesting during this period but when disturbed, would abandon the nest.

Diet

Recent analyses of stomach contents indicate that the Northern Madtom has a varied diet and is likely an opportunistic feeder. The stomach contents of 11 specimens from the Detroit River and one specimen from the Thames River were identified. Diet of the Detroit River specimens consisted primarily of chironomids, fish (Mimic Shiners, *Notropis volucellus*), mayflies, particularly *Hexagenia bilineata* and possibly *H. limbata*, crustaceans (Malacostraca, an ostracod, and an amphipod). In addition they contained smaller amounts of nematodes, Lepidoptera, and caddisflies (such as *Triaenodes aba, Hydropsyche scalaris*, and probably *Polycentropus*). The Thames River specimen contained mostly caddisflies (primarily *Potamyia flava* but one *Hydropsyche scalaris*) and mayflies (*Emphemerella* and probably *Stenonema*).

French and Jude (in press) described stomach contents of 25 adult Northern Madtoms (82-130 mm TL) captured inn the St. Clair River. These specimens were caught near Algonac State Park, Michigan, in May and June of 1994. They contained mostly mayflies (primarily *Baetisca* and occasionally *Hexagenia* and *Baetis*). Caddisflies (primarily represented *Phryganea*, *Banksiola* and a few *Hydropsyche*) were also present in substantial numbers. Midges of the family Chironomidae and Stoneflies (Plecoptera) were also represented to a lesser extent, and three small Round Gobies, *Neogobius melanostomus*, were found in the stomach of one specimen. The guts of juveniles (31-37 mm TL) collected at the same site contained mostly Diptera as well as numbers of mayflies (Ephemeroptera).

Species Movement

There is no published information on the movements or migration of the Northern Madtom.

Behaviour/Adaptability

The Northern Madtom probably feeds (Goodchild 1993) and spawns (Coad 1995) during the night. During diving transects in the Detroit River and Lake St. Clair, a few Northern Madtoms were observed off Peche Island at night, but none were seen during the day (B. Ray, University of Windsor, personal communication).

Limiting Factors

The restricted distribution and low numbers of the Northern Madtom suggests that it has specific ecological requirements (Goodchild 1993). The apparent persistence of populations of the Northern Madtom in the Detroit River, one of the most heavily polluted areas of the Great Lakes, suggests that it is relatively tolerant to human disturbance. However, the apparent absence of the Northern Madtom on the more polluted Canadian side of the St. Clair River (Griffiths et al. 1991) as well as the more polluted American side of the Detroit River (David Jude, personal communication) suggests that it avoids the poorer water quality of these rivers. Its northward dispersal may be limited by temperatures which are warm enough (e.g. 23°C) for spawning to occur. Global warming may allow the species to spread farther north. The rapidly expanding populations of Round Goby in Lake St. Clair and the Detroit River is threatening some native species such as the Mottled Sculpin, *Cottus bairdi* (Jude et al. 1996). Its impact on the Northern Madtom is not known.

Special Significance

Noturus species exhibit cryptic behaviour and possess poison glands associated with the pectoral spines that are unique to the Canadian fish fauna (Scott and Crossman 1973). One of the four *Noturus* species native to Canada, the Brindled Madtom, is listed by COSEWIC as Vulnerable (Campbell 1995) and we recommend a Vulnerable status for the Northern Madtom. Therefore, the genetic diversity expressed by behaviour, ecology and morphology in the genus *Noturus* may be in jeopardy in Canada.

Evaluation

The Northern Madtom is at the northern limit of its range in Canada. It has been found recently only in the Detroit River, Lake St. Clair and a tributary of Lake St. Clair, the lower Thames River. Although additional sampling is required to determine the stability, size and range of the species, it appears that reproducing populations are established in the

Detroit River, Lake St. Clair and the Thames River. These populations should persist if its habitat is not significantly altered.

There is no evidence of any other reproducing populations in Canada. Therefore, it should be recognized that, if these populations were extirpated due to human activity, the only known established Canadian populations of Northern Madtom would be lost. It is recommended that *Noturus stigmosus* be classified as Vulnerable in Canada.

Acknowledgments

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Status of the Bluntnose Minnow, *Pimephales notatus*, in Canada[†]

J. Houston

743 Fireside Drive, R.R.1 Woodlawn, Ontario K0A 3M0, Canada

Houston, J. 2001. Status of the Bluntnose Minnow, *Pimephales notatus*, in Canada. Canadian Field-Naturalist 115(1): 145–151.

The Bluntnose Minnow, *Pimephales notatus*, is a small cyprinid with a Canadian distribution from the upper St Lawrence drainage of southwestern Quebec west through southern Ontario to south eastern Lake Superior. It also occurs in the Lake-of-the-Woods region west of Lake Superior and other populations have been reported from two sites on the Winnipeg River and one site on the Red River of southeastern Manitoba. Although abundant where found in Ontario and Quebec it is rare in Manitoba.

Le ventre-pourri, *Pimephales notatus*, est un petit cyprinidé dont l'aire de répartition au Canada s'étend depuis l'amont du bassin versant du Saint-Laurent, dans le secteur sud-ouest du Québec, jusqu'à l'extrémité sud-est du lac Supérieur et englobe le sud de l'Ontario. On peut aussi trouver l'espèce à l'ouest du lac Supérieur dans la région du Lake-of-the-Woods et d'autres populations ont été signalées à deux sites dans la rivière Winnipeg et à un site dans la rivière Rouge, au sud-est du Manitoba. L'espèce est abondante, où on la trouve, en Ontario et au Québec, mais elle est rare au Manitoba.

Key Words: Cyprinidae, cyprinids, minnows, Bluntnose Minnow, ventre-pourri, *Pimephales notatus*, rare fishes.

The Bluntnose Minnow (Figure 1), *Pimephales notatus* (Rafinesque, 1820), is a small cyprinid (≈ 64 mm average length) occupying a broad range in central North America (Scott and Crossman 1973). It bears some resemblance to the Fathead Minnow (*Pimephales promelas*), Slim Minnow (*Pimephales tenellus*) and Bullhead Minnow (*Pimephales vigilax*) [Trautman 1957], the remaining three North American members of the genus (Smith 1979). However, only *Pimephales notatus* and *Pimephales promelas* are found in Canada (Scott and Crossman 1973).

In Canada it is abundant and widely distributed from southwestern Quebec west through the Great Lakes to the eastern end of Lake Superior and north to Temagami (Scott and Crossman 1973). It is also found in the Lake-of-the-Woods area in Ontario, and in Manitoba where it is known only from three localities (Keleher and Kooyman 1957; Scott and Crossman 1973).

This synopsis is a result of a request from officials of the Manitoba Department of Natural Resources to have the species considered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

Description

The Bluntnose Minnow (Figure 1) is a small cyprinid averaging 64 mm in length with an elongated, tubular body. The head is small, broad and bluntly triangular with moderate eyes; the snout is rounded and blunt giving rise to the common name and slightly overhangs the upper lip. The mouth is inferior, overhung by the snout, the gape does not reach the front of the eye; pharyngeal tooth count is 0,4-4,0. The dorsal fin of eight rays originates slightly behind the origin of the pelvic fins which also have eight rays; the caudal fin is moderately forked and rounded; the anal fin has seven (sometimes eight) rays and originates below the tip of the depressed dorsal; the pectoral fins are small with 15 rays but may have 14 to 17. The scales are cycloid, small and dense predorsally; the lateral line is complete with 42 to 50 scales. The peritoneum is black, the intestine is elongate and the vertebrae number 37 or 38 (see Scott 1967; Scott and Crossman 1973).

The fish are olive-green to brown dorsally, silvery on the sides and silvery white ventrally. The scales are dark-edged which gives a cross-hatched appearance which is particularly noticeable in young fish. A dark lateral band extends from the eye to a conspicuous black spot at the base of the caudal fin (Scott and Crossman 1973), the band is usually present around the snout, but may be less noticeable (Trautman 1957). Specimens from clear waters or areas with vegetation are usually prominently marked, those from turbid waters may be pale and lack the band and cross hatching (Trautman 1957). The fins are transparent, in older fish there may be a yellowish (Scott and Crossman 1973) or olive tint and the dorsal fin usually has a dark blotch on the two or three anterior rays (Trautman 1957).

Breeding males develop a thickened papilla like protuberance at each corner of the mouth, three rows of large, sharp nuptial tubercles across the

[†]Designated "Not at risk by COSEWIC April 1998.

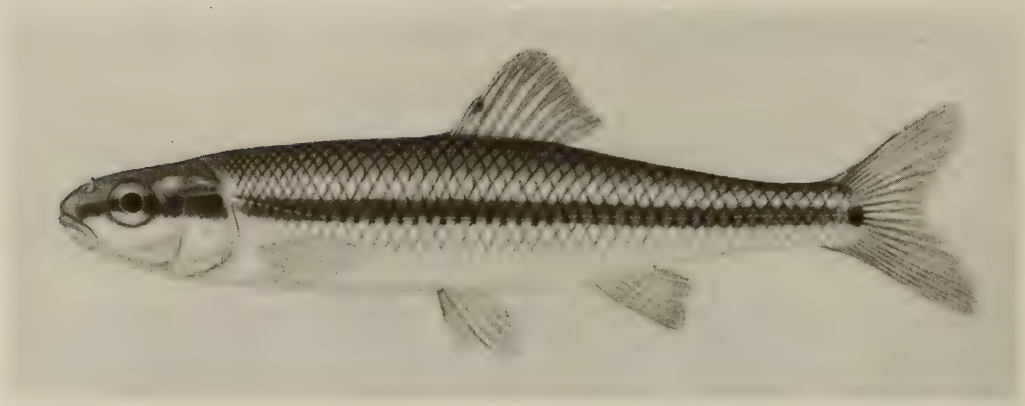

FIGURE 1. Bluntnose Minnow, *Pimephales notatus* [from Scott and Crossman (1973) by permission].

snout (Scott and Crossman 1973) and a spongy pad on the flatter, predorsal portion of the back, sometimes thick enough to hide the scales (Trautman 1957). The dorsal surfaces of the pectoral fins may also have tiny tubercles (Trautman 1957). The males become very dark, almost black during breeding, even the fins, particularly the dorsal fin are permeated with chromatophores (Scott and Crossman 1973).

The Bluntnose Minnow differs from the Fathead Minnow in that the Fathead Minnow has a terminal, oblique mouth; an incomplete lateral line; and is more yellowish in colour (Trautman 1957). It differs from other shiners with a black caudal spot in the crowded predorsal scales, elongate intestine and black peritoneum (Smith 1979).

Distribution

The species is native to central North America in the Mississippi and Great Lakes drainages (Figure 2). In the U.S., it ranges from eastern North Dakota east to New York, south to Virginia on the Atlantic slope, southwest to the Gulf States and north through the Mississippi basin to the Great Lakes (Scott and Crossman 1973; Lee and Shute 1980).

In Canada, the species has a somewhat disjunct distribution (Figure 2) representative of post-glacial dispersion (Hocutt and Wiley 1985). It is widely

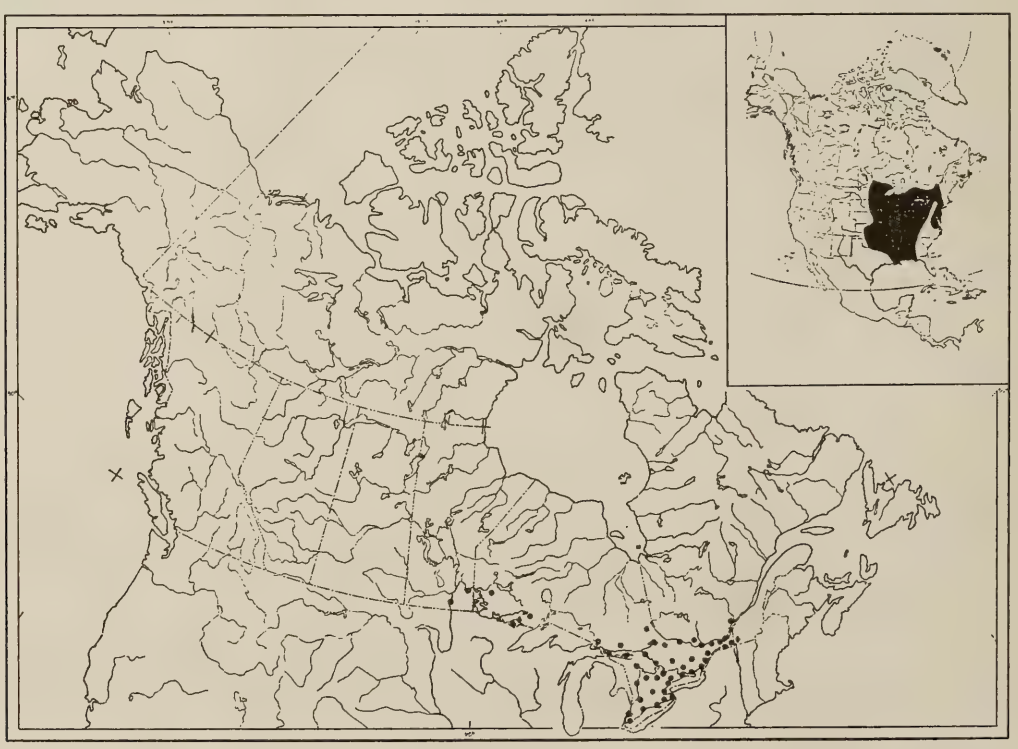

FIGURE 2. Canadian distribution of the Bluntnose Minnow, *Pimephales notatus* [from Scott and Crossman (1973) by permission].

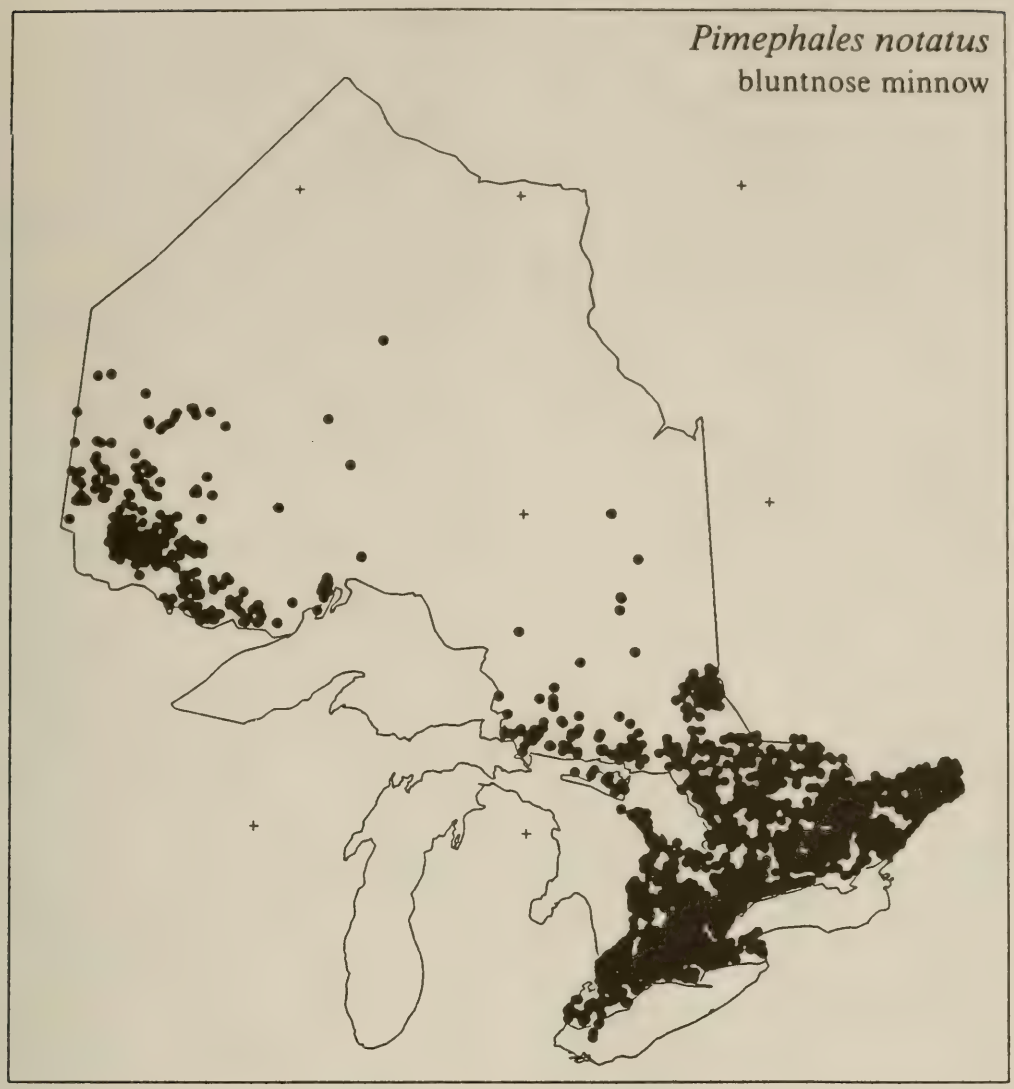

FIGURE 3. Distribution of the Bluntnose Minnow, *Pimephales notatus*, in Ontario [from Mandrak and Crossman (1992) by permission].

distributed from southwestern Quebec west through the Great Lakes to the Lake-of-the-Woods area in Ontario (Figure 3), and in Manitoba (Figure 4) where it is known only from three localities (Keleher and Kooyman 1957; Scott and Crossman 1973), two on the Winnipeg River, and one on the Red River.

Crossman and McAllister (1985) discuss possible post-glacial dispersion of the species into the Hudson Bay watershed from a Mississippi-Refugium.

Protection

The Bluntnose Minnow is not subject to any specific protection in Canada. The species has been considered to be of "special concern" in Manitoba (Johnson 1987), but has not as yet been considered for protection under the provincial Endangered Species Act.

In the United States, Bluntnose Minnows have been considered to be of "special concern" only in North Carolina (Johnson 1987).

Population Sizes and Trends

The Bluntnose Minnow is generally common where suitable habitat exists and is widely distributed in southwestern Quebec, southern Ontario and western Ontario (Lake-of-the-Woods), where it appears in most areas in sufficient numbers to be utilized as a bait fish (D. E. McAllister [Researcher Emeritus, Canadian Museum of Nature], Perth, Ontario K7H 3A0; personal communication). Although many streams have undergone habitat degradation similar to that responsible for the demise of other less sensitive cyprinids, the species may still be found at most sites where it has been known in this century and there is no evidence of a decline in the species in Ontario or Quebec [Collections at Canadian Museum of Nature, Ottawa; Royal Ontario Museum, Toronto; and Ontario Ministry of Natural Resources, Toronto; appendices of all records to 1990 have been deposited with COSEWIC at Canadian Wildlife Service, Ottawa).

In Manitoba, *Pimephales notatus* occurs in small

FIGURE 4. Distribution of the Bluntnose Minnow, *Pimephales notatus*, in Manitoba (after sources cited in the text).

numbers in the Winnipeg River above the Point du Bois Dam (50°18′N, 95°30′W) and vicinity, and Echo Lake, Whiteshell Provincial Park [ROM (Royal Ontario Museum) Number 14896]; as well as St. Andrew's Locks on the Red River (ROM 14896). Stewart (K. W. Stewart, Department of Zoology, University of Manitoba, Winnipeg, Manitoba; personal communication 1997) has examined the Red River specimens and confirms their validity. He feels that these were either waifs washed down the Winnipeg River, or more likely, released bait brought in from farther south. Apart from this anomalous collection Stewart (personal communication) indicated that there has been no downstream movement of *Pimephales notatus* in the Winnipeg River. Scott and Crossman (1973) reported that the species was rare in Manitoba. Stewart (personal communication) believes that the species is of concern in Manitoba only because of its extremely restricted range. Although not abundant in the Winnipeg River above the Point du Bois Dam it can be collected there with some predictability.

Habitat

The Bluntnose Minnow is a resilient species occurring in almost all types of waters within its natural range except the deeper waters of lakes and rivers (Trautman 1957). It prefers hard-bottomed, sandy or gravelly shallows of pools in creeks and small rivers, but may be found elsewhere, except (and as previously noted) in swamps, heavily weeded areas and heavily silted ditches and ponds (Scott and Crossman 1973; Smith 1979). The Bluntnose Minnow appears to be able to survive in areas where there is high competition from a number of other species and can inhabit waters with gradients of 0 to 15 m/km, although its abundance is limited where the gradient is more than 9 m/km or where there is intense competition, especially with Fathead Minnows. It has a high tolerance to siltation and turbidity, and organic and inorganic pollutants, but is less abundant in excessive turbidity and siltation or extreme (high and low) pH values (Trautman 1957). Schlosser (1985) found that the species was more successful in stable flow regimes and was less abundant in periods of above normal flow conditions.

Stauffer et al. (1984) found that the species could tolerate water temperatures in the range of 6 to 36°C with a preferred temperature of 26.3°C. Cherry et al. (1977) found the preferred temperature to be 28.4°C in Virginia. Spawning usually occurs when water temperatures reach 20°C (Scott and Crossman 1973).

It apparently will spawn just about anywhere in shallow waters and will migrate up the smallest temporary brook to spawn. Males build nests around spawning objects which may be just about anything including the underside of stones, boards, logs, tin cans leaves or other objects that are not easily silted over (Trautman 1957; Scott and Crossman 1973).

Bluntnose Minnows can be successfully artificially propagated in ponds, especially where artificial nesting sites are provided (Cooper 1936; Dobie et al. 1956; Trautman 1957; Scott and Crossman 1973).

General Biology

Reproduction

Spawning commences in May to June when water temperatures reach 20°C and is prolonged (into August) in some areas (Toner 1943; Scott and Crossman 1973). Spawning ceases when water temperatures fall below this minimum and does not commence again until a few days after the minimum is reached. Higher temperatures also lead to cessation of spawning (Gale 1983). Not all spawning occurs at one time. Nests may contain eggs in various stages of development and the ovaries of females contain 1700 to 2200 eggs in various stages of maturation (Westman 1938; Scott and Crossman 1973). Gale (1983) and Westman (1938) found the spawning usually occurs at night, but it may occur during the day (Hubbs and Cooper 1936). Captive females

deposited an average of 93 to 239 eggs per session, intervals between sessions lasting two to 14 days (Gale 1983). Minnows in the wild spawned at intervals of two to eight days (Westman 1938) laying 25 to 100 eggs per session, each session lasting 10 to 30 minutes (Hubbs and Cooper 1936). Gale (1983) reported that captive females spawned seven to 19 times over the spawning season (May to August) producing a total of 1100 to 4200 eggs; Westman (1938) noted that a pair in a 500 m^2 pool spawned 12 times and produced 2300 eggs. Gale (1983) surmised that fecundity was unrelated to body size.

The eggs are large, 1.0 - 1.5 mm in diameter, adhesive and deposited in a nest on the undersurface of submerged or floating objects where they are guarded and aerated by the male (Scott and Crossman 1973; Smith 1979; Gale 1983). Westman (1938) found that the male's presence is essential to ensure a steady flow of water and oxygen over the eggs and to keep them free of silt by the movement of the water and by cleaning the eggs with the spongy tissue on the nape (Trautman 1957). The eggs hatch in 7 to 14 days depending on water temperature (Scott and Crossman 1973).

Growth

Fish (1932) provided a detailed description of the eggs and young at lengths of 5 mm (newly hatched), 6 mm (seven days old) and 12 mm [two weeks after hatching (Westman 1938)]. Growth depends on water temperature and food abundance (Mahon and Ferguson 1981). They may attain a length of 55 mm by the end of their first growing season in New Jersey (Westman 1838). Mahon and Ferguson found young of the year raised in a reservoir at Guelph, Ontario averaged 33.3 mm S.L. [Standard Length] as compared to 27.6 mm S.L. for those taken at the Speed River in Guelph at the end of the growing season. Trautman (1957) reports that young of year in Ohio may reach lengths of 71 mm depending on date of hatching and year-old-fish 72 mm. Females reach maturity in their second year and males in their third year. Longevity is not known, but three-year-old fish have been taken. Males grow faster than females and may attain a length of 102 mm (New Jersey), while females reach 76 mm (Scott and Crossman 1973). Trautman (1957) noted greatest length in Ohio at 108 mm and Smith (1979), found a maximum of 90 mm in Illinois.

Diet

The Bluntnose Minnow is a generalized bottom feeder and the diet consists of organic detritus, algae, plankton, aquatic vegetation and insect larvae (Scott 1967; Scott and Crossman 1973; Smith 1979; Lee and Shute 1980). The inferior mouth is an adaptation to bottom feeding (Scott and Crossman 1973). Individuals from Kearney Lake, Algonquin Park, Ontario, fed mainly on chironomid larvae and algae (Scott and Crossman 1973), whereas Keast and Webb (1966) found that fish from Lake Opinicon, Ontario, relied on bottom ooze, chironomid larvae and Cladocera, in that order. Keast (1985) also found that the Bluntnose Minnows in Lake Opinicon were seasonal, specialized planktivores and that *Chydorus sphaericus*, was the main zooplanktor taken, regardless of abundance. Morgan and Colgan (1988) found that näive school members begin to feed more quickly on a new food source when experienced school members are present.

Behaviour

Spawning

The male selects a suitable stone or other object resting on the bottom in 0.15 to 1 m of water and excavates a depression beneath the object and cleans its undersurface with his tail and horny snout. The males do not seek out females and will only allow a female to enter the nest when it is completed. The adhesive eggs are deposited on the underside of the object and fertilized by the male (Trautman 1957; Scott and Crossman 1973; Smith 1979). The males are territorial and aggressive and guard the nest until after all eggs have hatched; they will permit additional females to deposit eggs, but drive away other intruders (Smith 1979). Up to 5000 eggs have been found in a single nest (Hubbs and Cooper 1936). The nesting territory may be small when large objects are available; Hubbs and Cooper (1936) reported that long boards could have one nest per linear foot.

The males also clean the eggs with the spongy tissue on the nape which keeps them from being suffocated by silt. Males also provide oxygen by moving water over the eggs with their tails (Trautman 1957). If the male is removed from the nest the eggs will die within 12 hours (Westman 1938).

Ming and Noakes (1984) found that Bluntnose Minnow males dominate Fathead Minnows in selection and defence of spawning sites because of their larger size and inherent aggressiveness where adequate spawning sites (near the substrate) are available. If spawning sites are scarce, the Fathead Minnows may dominate Bluntnose Minnows. They also found that interspecific dominance was not a factor of size or maturity and that codominance may occur where there are plenty of spawning sites.

Movement

Bluntnose Minnows segregate into localized groups of similar-sized individuals (Becker 1983). In the presence of predators, the incidence of size segregation increases; smaller fish move to the centre of the school leaving larger fish on the outside (Theodorakis 1989), thereby reducing the risk of predation to the smaller individuals.

In spring, mature fish migrate into shallower waters (0.15 to 1 m) to spawn. Schlosser (1985) indicated the importance of spring flooding in second-order streams for spawning and Trautman (1957)

noted their habit of migrating up small, temporary streams to spawn. The adults and young return to deeper, permanent waters before the temporary streams dry up (Trautman 1957).

Predators/Parasites

The Bluntnose Minnow is an important forage fish for game fishes, particularly Yellow Perch (*Perca flavescens*), sunfishes (*Lepomis* spp.), Rock Bass (*Ambloplites rupestris*), Smallmouth Bass (*Micropterus dolomieu*) and Largemouth Bass (*Micropterus salmoides*), and other centrarchids (Scott and Crossman 1973). The species is cannibalistic as young males will devour the eggs in unprotected nests (Scott and Crossman 1973).

The trematodes, *Uvullifer* sp., *Uvullifer vancleavi*, and *Lebouria cooperi*; the cestode *Ligula intestinalis*; Protozoa and Mysosporidia have been found on Bluntnose Minnows from Lake Erie (Bangham and Hunter 1939). Specimens from Lake Huron were infected with the trematodes including *Posthodiplostomum minimum*, protozoans and the nematode *Rhabdochona cascadilla* (Bangham 1955). Hoffman (1967) lists many species of Protozoa, Trematoda, Cestoda, Nematoda, molluscan glochidia and the crustacean *Lernaea cyprinacea* as parasitic of the species in North America. Hockett (1988) found that parasite loads of metacercariae (*Uvulifer* sp.) had no effect on the growth or thermal tolerance of the species.

Pot and Noakes (1985) found that individual Bluntnose Minnows could be recognized by means of the pattern of spots caused by trematode cysts.

Limiting Factors

Although it is not particularly sensitive to turbidity and siltation (Trautman 1957), the species is least abundant in areas of excessive turbidity and with high rates of siltation; in waters of extreme pH values, acid or alkaline; where the gradient is greater than 9 m/km high. It is also less abundant in areas where there are large concentrations of predators or competitors such as the Fathead Minnow (Trautman 1957).

Special Significance

The Bluntnose Minnow is an important forage fish for game fishes, particularly centrarchids and uses a food source not exploited by predacious fishes. It is also used for live bait in Canada and the United States, but does not take well to crowding in a pail (Trautman 1957; Scott and Crossman 1973; Cooper 1983).

Its broad distribution and abundance may be related to the fact that it occupies habitat not usually inhabited by other species, and can survive in low numbers under extreme competition. The species is tolerant of turbidity and siltation and does well in streams of very low gradient (Trautman 1957).

The disjunct distribution and habitat requirements are of interest to science in relation to the zoogeographic history and possible dispersal of fish subsequent to the Wisconsin glaciation.

Evaluation

The Bluntnose Minnow is abundant and widely distributed in Canada from southwestern Quebec to the eastern end of Lake Superior. It is known only from three sites in Manitoba on the Red River, the Winnipeg River, and Echo Lake of the Winnipeg-Rainy River system. It is also found in the Lake-of the-Woods area in Ontario. The western distribution in Ontario is probably the result of postglacial dissemination from a Mississippi Refugium. Its rarity and restricted range in Manitoba where it is known from only three locations has lead to it being considered a species of concern there (Stewart, personal communication), but it appears to be abundant and not at risk elsewhere in Canada.

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Status of the Texada Stickleback Species Pair, *Gasterosteus* spp., in Canada†

J. HOUSTON

743 Fireside Drive, R.R.1, Woodlawn, Ontario K0A 3M0, Canada

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A sympatric pair of stickleback species (*Gasterosteus* spp.) occur in Paxton Lake on Texada Island, British Columbia. These species are reproductively isolated and adapted to alternate trophic niches. One form (benthic) is a littoral, benthic forager, whereas the other (limnetic) is a pelagic plankton feeder. The benthic member is larger (90 mm Standard Length), with a short body, wide mouth relatively few, short gill rakers, and a reduced number of lateral plates and dorsal spines. The entire pelvic girdle is absent in about 80% of adults. The limnetic form is smaller, slim, small-mouthed, with long gill rakers and normal lateral plates, dorsal spines, and pelvic girdle. Crosses breed true, suggesting the forms represent distinct gene pools. Genotypic and phenotypic characteristics have remained stable for over 20 generations with less than 1% incidence of hybridization which indicates that gene flow between the forms is negligible and that the forms behave as biological species. Although both forms are numerous, they are restricted to one small (17 ha) lake which is used for a source of water for industry. In the short term the species could be threatened by the introduction of other fishes and in the long term by water draw down and further industrial development.

On trouve dans le lac Paxton sur l'île Texada, en Colombie-Britannique, deux espèces sympatriques d'épinoche (*Gasterosteus* spp.). Ces espèces sont isolées du point de vue reproductif et adaptées à des niches trophiques alternatives. La forme benthique est surtout littorale et se nourrit de benthos tandis que la forme limnétique est planctivore et vit dans la zone pélagique. La forme benthique est plus grande (90 mm de longueur standard), a un corps trapu, une bouche large, des branchicttures courtes et relativement peu nombreuses, et un nombre réduit de plaques latérales et d'épines dorsales. La ceinture pelvienne est absente chez 80% des adultes. La forme limnétique a un corps mince, une bouche étroite, de nombreuses branchicténtes longues et des plaques latérales, des épines dorsales et une ceinture pelvienne normale. Dans les expériences de croisements, les formes ne donnent pas d'hybrides et cela indique qu'elles représentent des pools génétiques distincts. Les caractères génotypiques et phénotypiques sont restés stables pendant plus de 20 générations avec moins de 1% d'hybrides. Ceci indique que le passage de gènes entre les deux formes est négligeable, et que les deux formes se comportent comme des espèces biologiques. Les populations des deux espèces sont élevées, mais elles sont confinés à un petit lac (17 ha) du lequel on prélève l'eau pour l'industrie. À court terme, les espèces pourraient être menacées par l'introduction d'autres espèces de poissons, et à long terme par l'utilisation industrielle de l'eau et une augmentation du développement industrielle.

Key Words: Gasterostidae, sticklebacks, *Gasterosteus*, Threespine Stickleback, Texada Island, *d'épinoches de Texada*, Paxton Lake, British Columbia, endangered fishes.

The Threespine Stickleback (*Gasterosteus aculeatus* Linnaeus, 1758) is widely distributed in temperate marine and fresh waters and cooler coastal waters throughout the northern hemisphere. Within this vast range there is a plethora of ecological forms and morphologically distinct geographic isolates (McPhail 1989, 1992a). The taxonomy of the genus is chaotic (Miller and Hubbs 1969; Hagen and McPhail 1970) and the only thing that is certain is that *Gasterosteus aculeatus* is not a single species, but a complex of species (McPhail and Lindsey 1970; Bell 1976).

Description

The nominate species, the Threespine Stickleback is a small fish [averaging 51 mm Standard Length (S.L.)] with a laterally compressed, elongate body tapering to a slender acaudal peduncle. There are usually three to four branchiostegal rays; a dorsal fin consisting of three isolated, short serrated spines, the last being shorter, preceding 11 to 13 soft rays. The pectoral fins are large and located laterally behind the gill opening; the pelvics are thoracic and ventral, each with one spine and one soft ray. The body is plated with a variable number of vertical, oblong pates on each side. These may be numerous (30 or more) on marine specimens, but are usually few to none on freshwater forms. The lateral line is complete and high on the sides (*see* Scott and Crossman 1973).

The colour of these forms varies, depending on habitat, from silvery green to grey, olive, greenish brown, to black. The sides are lighter with silvery reflections and the belly silvery. The fins are transparent, but may have a red tinge. During the breeding season mature males may be brilliantly coloured

†Threatened status assigned by COSEWIC April 1998.

with red bellies and flanks, and blue eyes; females may assume pink tints on the throat and belly. The larvae are yellowish and young fish silvery (see Scott and Crossman 1973).

There is tremendous morphological variability within the species (see Hagen and McPhail 1970). Marine forms have a complete series of bony plates, are silvery in colour, larger in size, and are anadromous. Freshwater forms are smaller, have reduced, but variable numbers of plates and spend their lives entirely in fresh water (Scott and Crossman 1973). A particularly remarkable diversity has evolved in the freshwater populations of British Columbia (and Washington) in relation to the isolation of the lakes in which they are found and the speed with which the isolates react to local selective regimes (see later discussion under Special Significance).

In these lake populations there are inherited differences in size, colour, spines, plate numbers, gill raker length and numbers, and mouth size (McPhail 1992a). Although the trophic morphology reflects an evolutionary response to a local foraging regime, McPhail (1989; 1992b), and others (Moodie and Reimchen 1976; Reimchen 1984a,b; Reimchen et al. 1985) have shown that at least some of these forms (e.g., Enos, Boulton, Rouge, Serendipity and Mayer lakes), including the species pair found in Paxton Lake, Texada Island, are distinct (but unnamed) species and not part of a large gene pool containing a foraging polymorphism.

Recently McPhail (1992b) described the two sympatric forms from Paxton Lake. They are reproductively isolated, genetically discrete and adapted to exploit alternate trophic niches, filling all the requirements of biological species (Mayer 1963). At present the least confusing way to refer to these animals is simply the Texada or Paxton Lake Stickleback species pair. A formal taxonomic designation must await a detailed examination of their relationship to other divergent forms of *Gasterosteus*.

The benthic form (Figure 1) is larger (up to 90 mm S.L.) than the nominate (51 mm) or limnetic form which averages 45 mm S.L. Benthic fish are stouter, have wider mouths, fewer gill rakers and a reduced number of lateral plates and dorsal spines, in about 80% of adults the pelvic girdle is missing (*see* McPhail 1992b: his Tables 3,4). On the other hand, the limnetic fish (Figure 1) are more like the nominate form, slim bodied, narrow mouth, numerous big gill rakers, and normal lateral plates and dorsal spines and a normal pelvic girdle (see McPhail 1992b: his Tables 3,4).

Distribution

The Texada Stickleback species pair is restricted to Paxton Lake (49°42'30"N, 124°31'30"W), Texada Island, British Columbia (Figure 2). Two other lakes (Myrtle and Cove) downstream of Paxton Lake and Rumbottle Creek contain sticklebacks similar to the benthic form and these may be derived from Paxton Lake benthics (McPhaill 1992b; Cannings 1993). Of the eight other lakes on the island containing sticklebacks, only Paxton Lake contains girdleless fish (McPhail 1992b).

Protection

Currently the fish are not subject to any protected status and could not qualify for general protection under Habitat Sections of the Fisheries Act (not commercial species). General protection could be afforded if required under British Columbia provincial wildlife and endangered species legislation.

Population Sizes and Trends

Both forms are numerous in the lake, the total population of each probably exceeding 10 000 individuals (Cannings 1993), but there is no data on which to base trends in population size. The populations are probably more or less stable at this time (McPhail 1992b), but probably fluctuate over time. McPhail (1992b) suggests this has happened in the past since 5% of the limnetic fish are girdleless, and postulates that this has arisen through gene flow from the benthics at a time when the density of parental forms was biased towards the benthic fish.

Habitat

Paxton Lake is a small (17 ha) lake with a maximum depth of about 15 m (Figure 3). The lake is about 90 m above sea level and the only outlet, Rumbottle Creek, drops about 80 m in a series of small falls in its last two km before entering Malisipina Strait and thus isolating the upper portions of the creek and the lake from the sea. There is no permanent surface flow into the lake and the outlet was dammed in 1956 to provide water for a nearby iron mine. This increased the lake level by 1.5 m. Apparently, before damming of the outlet the lake consisted of two lakes joined by about 100 m of stream at the North Rockface (Figure 3). The lake now has two equal basins connected by a narrow channel (McPhail 1992b). The lake lies in limestone on postglacial marine sediments and the substrate, especially at the south end is marl (Larson 1976). The annual drawdown now appears stable at about 1 m (McPail 1992b), but from 1957 to 1979 was approximately 3 m (Larson 1976; McPail 1992b).

Summer water temperature may reach 23°C with a thermocline between 2 to 5 m, hydrogen sulphide may be detected below 7 m in summer, *Chara* is the dominate vegetation in the littoral zone (Larson 1976).

Benthic fish occur in open, mud-bottomed situations, above the deoxygenated zone, and smaller fish (< 50 mm) are usually to be found in shallower water. They prefer some cover and are often found

FIGURE 1. Paxton Lake Sticklebacks. (A) Limnetic male (45.3 mm S.L.). (B) Benthic male (45.9 mm S.L.). Reproduced from McPhail (1992b) by permission.

around sunken logs. Spawning occurs in shallower waters of the littoral zone and nests are usually found under cover in aquatic vegetation (Larson 1976).

The limnetics form large aggregations near the surface in the littoral zone during the day, usually in areas with surface cover (trees, leaves, etc.,) or in tall vegetation above Chara. They appear to migrate offshore at dusk and in winter are found on the lake bottom. Spawning occurs in open areas in the littoral zone devoid of cover (Larson 1976).

Biology

The only published account of the biology of the species pair is that of Larson (1976). Both species show the typical *Gasterosteus* life cycle and behaviour (see Scott and Crossman 1973). They do differ in their feeding behaviour, spatial distribution and seasonal habits. The limnetic form is a pelagic plankton feeder concentrating on zooplankton, mainly cladocera; whereas the benthic form is a benthos feeder, feeding mainly on amphipods (*Gammarus* sp.), midge larva (Chironomidae) and ostracods. Some small individuals feed partially on plankton (Larson 1976). During the sumer the limnetic species occurs near the lake surface and moves to deeper water in winter. The benthic species occupies the littoral zone in summer and disperses over the entire lake bottom in winter.

The species pair are the only fish which breed in the lake. Cutthroat Trout (*Oncorhynchus clarki*) are also native to the lake, but have virtually disappeared since the outlet stream was dammed in 1956, there being no trout spawning site in the lake itself (McPhail 1992b). There are sticklebacks intermediate between the two forms, but these are not abundant (1 to 2 %) and their morphology and behaviour probably puts them at a disadvantage relative to the parental forms (McPhail 1992b).

The majority of sticklebacks in the lake can easily be separated by eye into benthic and limnetic types; the terms allude to the two major habitats used in the lake and do not necessarily imply a relationship with benthic or limnetic forms in other lakes. The two forms differ in morphology (number of dorsal spines and body plates, presence of pelvic girdles and spines, and number of gill rakers — *see* Description above and McPhail 1992b). Benthics are larger and more aggressive and frequently chase the limnetics forcing them to seek cover above the Chara.

The sticklebacks of Paxton Lake have been under intermittent study since 1968. The differences in morphology and allelle frequencies between the two forms have remained stable during the period of study with about 1% incidence of hybridization McPahil 1992b). In laboratory crosses the two forms breed true indicating the two forms represent separate gene pools.

Limiting Factors

Water from the lake is used for industrial purposes. At present the annual drawdown is about 1 m, but in the past has been as much as 3 m (McPahil 1992b). If larger drawdowns occur the populations

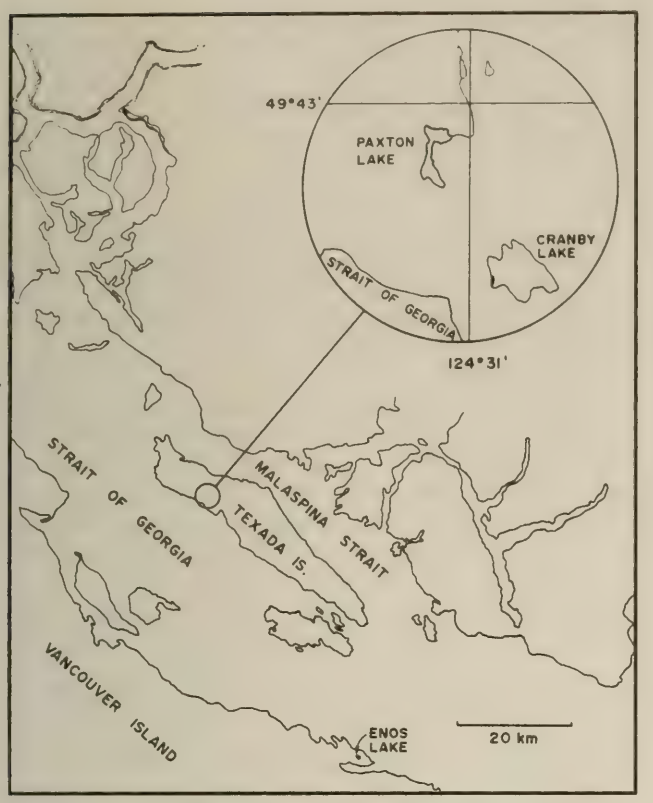

FIGURE 2. Paxton Lake, Texada Island, and the Strait of Georgia. Reproduced from McPhail (1992b) by permission.

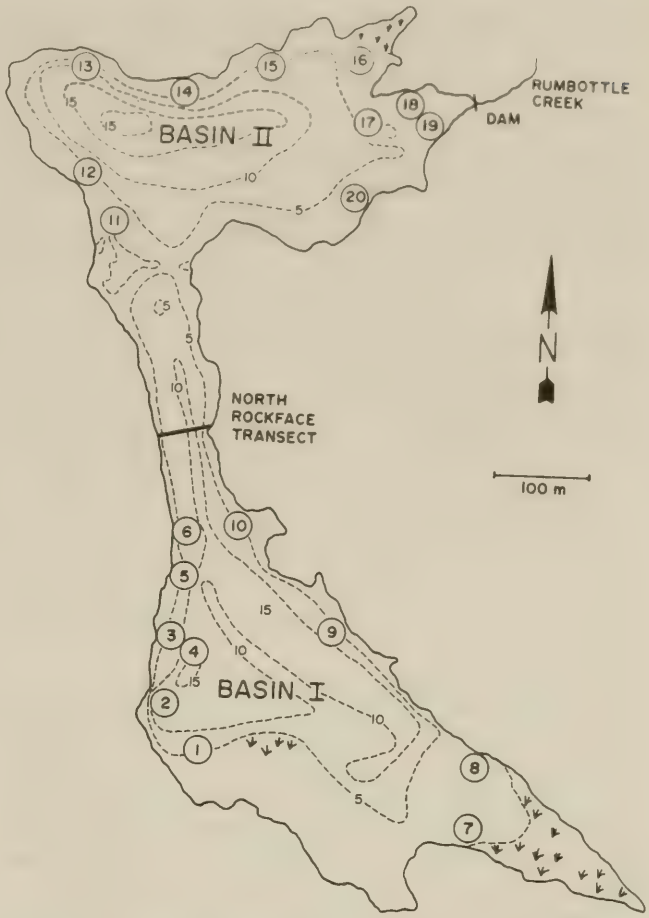

FIGURE 3. A bathymetric map of Paxton Lake, showing the two basins, and key (collection) sites. Reproduced from McPhail (1992b) by permission.

could be adversely affected by subsequent changes in the ecology of the lake.

The only known predator is the Cutthroat Trout which is also native to the lake. These have all but disappeared since the outlet stream was dammed in 1956, there being no trout spawning site in the lake (McPhail 1992b). However, local people still occasionally introduce trout.

Coho Salmon (*Oncorhynchus kisutch*) where introduced into the lake in 1968 and were significant predators. They did not breed however, and by 1973 were extirpated (McPail 1992b).

A major threat to these small B.C. lakes is the introduction of exotic species, especially Catfish (*Americanus nebulosus*) and Pumpkinseed (*Lepomis gibbosus*). The introduction of such exotics has apparently led to the extinction of at least one species pair in Hadley Lake (R. Campbell, Chairman, COSEWIC Subcommittee Fish and Marine Mammals, Ottawa, Ontario; personal communication).

Special Significance of the Species

The sympatric populations of Threespine Sticklebacks in Paxton Lake provide excellent material for the study of speciation. What is remarkable about the Paxton Lake pair is the rapidity of the event (less than 12 500 years, see McPahil 1992b) and the relatively short period of geographic isolation. The morphological, ecological and behavioural differences that occur between members of the pair evolved within the lake. This *in situ* evolution and the rapidity of its occurrence makes the species pair unique.

Evaluation

The stickleback species pair of Paxton Lake is one of very few such pairs in the world. All of these are confined to the Strait of Georgia region of southwestern British Columbia. The Paxton Lake forms meet the criterion for biological species (Mayr 1942; McPahil 1992b), but final taxonomic recognition awaits a complete revision of the genus (McPhail 1989). This does not negate the responsibility to protect unique populations where there is compelling evidence for more than one species such as in Paxton Lake.

The species pair is restricted to one small lake, susceptible to exotic fish introductions, urban and industrial development and water drawdown for industrial use. They should be considered threatened as was done in the case of the Enos Lake species pair (McPhail 1989).

Acknowledgments

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Updated Status of the Central Stoneroller, *Campostoma anomalum*, in Canada†

E. Holm and E. J. Crossman

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario M5S 2C6, Canada

Holm, E., and E. J. Crossman. 2001. Updated status of the Central Stoneroller, *Campostoma anomalum*, in Canada. Canadian Field-Naturalist 115(1): 157–167.

The Central Stoneroller was known in Canada from only two areas in Ontario when it was classified as Vulnerable in 1985. It has continued to expand its range not only where it was originally found in the Thames River drainage, but also throughout southern Ontario. It is now known from the extreme southwestern end of Ontario near Kingsville, east to a tributary of the Rideau River near Perth, and north to a tributary of southern Georgian Bay near Midland. This ecologically important herbivore has the potential to make profound changes in the stream flora and fauna where it occurs in abundance. Moderately tolerant to stream degradation and abundant throughout most of its North American range, this large minnow should now be considered as Not at Risk in Canada.

Key Words: *Campostoma anomalum*, Central Stoneroller, Cyprinidae, roule-caillou, Vulnerable.

The Central Stoneroller, *Campostoma anomalum* (Rafinesque, 1820), was assigned a status of Rare (= Vulnerable) in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1985 based on its limited and isolated distribution in the North Thames River in southwestern Ontario. Although a range expansion was evident in 1979, McAllister (1987) recommended that the species deserved some level of protection in Canada because the expansion may have been temporary and the streams in the agricultural areas where it occurred were "exposed to pesticide spills and other environmental disasters". This report provides updated information on the continuing spread of the species both in the Thames River drainage and in many other river systems of southern Ontario. A summary of recent information from research on the ecology and biology of the Central Stoneroller is also presented.

Taxonomy and Description

Campostoma anomalum (Figure 1) is the most common and widespread of four species currently recognized in the genus (see Page and Burr 1991). Careful examination of the lower jaw with a probe will reveal a distinctive white cartilaginous ridge which is an important diagnostic character of the species. It is also distinguished from other Canadian cyprinids by its extremely long gut that is coiled around the swim bladder. Spawning males of the Central Stoneroller are very distinctive, having numerous tubercles on the head and back and a black band on the orange dorsal and anal fins (Figure 1, top).

Since it was only relatively recently discovered in Canada, *Campostoma anomalum*, has probably been frequently misidentified and therefore missed in surveys of fishes. It was not included in the widely used key to minnows in Scott and Crossman (1973). If that key is used, specimens of the Central Stoneroller would probably key out to the Brassy Minnow (*Hybognathus hankinsoni*). It has also been known to be confused with Blacknose Dace (*Rhinichthys atratulus*), River Chub (*Nocomis micropogon*), Hornyhead Chub (*Nocomis biguttatus*), and juvenile suckers (*Catostomidae*) (personal observations; McAllister 1987; Gruchy et al. 1973).

Currently three subspecies of *Campostoma anomalum* are recognized but the variation in the species is unclear (Burr 1980; Page and Burr 1991; Jenkins and Burkhead 1994). *Campostoma anomalum michauxi* from Virginia (Jenkins and Burkhead 1994) and the Carolinas lacks a black band on the anal fin of breeding males (Page and Burr 1991). The usual concept is that the individuals found in Ontario should be *Campostoma anomalum pullum*. Most character values of 24 Canadian specimens (Table 1) approximate those for *Campostoma anomalum pullum*, although circumferential, dorsal circumferential, and predorsal scale counts tend to be slightly lower than those described by Burr (1978) for Illinois populations.

Larval characteristics and development of *Campostoma anomalum* from the Susquehanna drainage near Berwick, Pennsylvania were described by Buynak and Mohr (1980). However, identification of specimens less than 20–30 mm is unreliable.

†Reviewed and Approved by COSEWIC, April 1998, Not At Risk (formerly Vulnerable — April 1985).

FIGURE 1. Central Stoneroller *Campostoma anomalum*: upper, ♂ 99 mm TL; lower ♀ 91 mm TL (Copyright 1987, Joseph R. Tomelleri).

Distribution

Campostoma anomalum is widespread and ubiquitous throughout much of eastern and central United States (see Figure 2). Older records of this species from Alabama, Georgia and Tennessee recorded by Burr (1978) have been reidentified as the Largescale Stoneroller, *Campostoma oligolepis* (Page and Burr 1991; Boschung 1992; Brooks M. Burr, personal communication). *Campostoma anomalum* is found in the Red River in North Dakota and Minnesota (Burr 1980) and therefore would have access to streams in Manitoba. It would be expected to show up first in the Rat and Roseau rivers where some limited sampling has been done but no Central Stonerollers have been found (Ken Stewart, personal communication).

McAllister (1987) reported the Central Stoneroller from only two areas of Ontario. There was a well-established population occupying a 25 × 45 km portion of the Thames River drainage between London and Mitchell and there were two records from the Niagara River around the mouth of Frenchman's Creek (see open circles, Figures 3 and 4). *Campostoma anomalum* was first discovered in Canada in 1972 in the North Thames River approximately 125 km from the nearest populations in Michigan (Gruchy et al. 1973). McKee and Parker (1982) noted a considerable expansion of range between 1972 and 1979 in the North Thames River and the population was maintaining itself in 1982 (McAllister 1987). The Niagara River records consist of two immature specimens of *Campostoma anomalum* captured in 1977 in stream surveys conducted by the Ontario Ministry of Natural Resources (OMNR). No subsequent captures of the species have been made in the Niagara River or its tributaries.

Records reported by McAllister (1987) appear as open circles in Figures 3 and 4 and new records are indicated by solid squares. In order to follow through time the spread of the species, the dates at which the species was collected from new locations were tabulated (Table 2). Table 2 and the distribution maps have been prepared from records (which are on file with the COSEWIC Secretariat, Canadian Wildlife Service, Ottawa, Ontario K1A 0H3) compiled from a variety of sources including the OMNR, Royal Ontario Museum (ROM), Canadian Museum of

TABLE 1. Characteristics of the two common subspecies of *Campostoma anomalum* and a sample of Canadian specimens.

Character	*C. a. anomalum*	*C. a. pullum*	Canadian specimens
pectoral rays	15–16[1]	16–19[1]	17–19 ($\bar{x}$=18, n=24)
lateral line scales (lls)	45–51 ($\bar{x}$=48.2, n=51)[2]	46–63 ($\bar{x}$=50.8, n=875)[2]	48–56 ($\bar{x}$=51, n=24)
circumferential scales (cs)	34–41 ($\bar{x}$=37.6, n=51)[2]	36–50 ($\bar{x}$=41.9, n=876)[2]	36–43 ($\bar{x}$=40, n=21)
lls+cs	83–91 ($\bar{x}$=85.8, n=51)[2]	85–108 ($\bar{x}$=92.7, n=874)[2]	87–98 ($\bar{x}$=91.0, n=21)
dorsal circumferential scales	15–17[3]	18–20[3]	17–19 ($\bar{x}$=18, n=24)
predorsal scales	18–23 ($\bar{x}$=19.5)[2]	20–27 ($\bar{x}$=23.0)[2]	19–24 ($\bar{x}$=21, n=18)
gill rakers	21–29 ($\bar{x}$=24.9, n=14)[2]	26–35 ($\bar{x}$=30, n=31)[2]	24–34 ($\bar{x}$=29, n=20)
gape width	44–58 ($\bar{x}$=50)[4]	44–60 ($\bar{x}$=55)[4]	48–65 ($\bar{x}$=56.5, n=23)

[1]According to Page and Burr (1991)
[2]According to Burr (1976) for Illinois populations
[3]Dorsal circumferential scales (from Page and Burr 1991: 94): scales over the body from lateral line to lateral line at the dorsal origin (including lateral-line scales)
[4]Thousandths of SL according to Burr (1976) for Illinois

Nature (NMC), Conservation Authorities, educational institutes, and private consultants. The species was recorded in 1978 in a small Essex County stream (Mill Creek) near Kingsville. Fieldwork in 1996 confirmed the existence of the population in Mill Creek and found the Central Stoneroller in two additional streams just to the west. These records represent the western limit of the species in Ontario. In the Ontario portion of the Lake Huron drainage, it was first recorded in 1980 and has recently been reported from municipal drains of the upper Maitland River. In 1984 the species was discovered in the Rouge River in Metropolitan Toronto and has since spread throughout that system and into neighbouring streams. Although we have seen only one specimen from the Lindsay area (from Sturgeon Lake), it is apparently well established in the Scugog River, and its tributaries Jenning's Creek, McLaren Creek, and Mariposa Brook (Ted Warren, Sir Sandford Fleming College, personal communication). The species is also known from an area around Kaladar in central Ontario (see "?" symbol on Figure 3). A single specimen captured from a Tay River tributary in Lanark County represents the eastern limit of the known range of the species in Canada and specimens captured from Stothart Creek (see Table 2) represent the northern limit of the species in Ontario.

The range of the Central Stoneroller in the Thames drainage has continued to expand. It is now known from there as far downstream as Tates bridge 27 km SW of London and upstream to a Thames tributary near Woodstock, 42 km northeast of London (Figure 4). Since it is often misidentified, however, the range of the Central Stoneroller may be greater than our records indicate.

Campostoma anomalum has been considered native to Ontario (Gruchy et al. 1973; Mandrak and Crossman 1992; and Litvak and Mandrak 1993). Its distribution in the southern half of the Michigan peninsula (Burr 1980) suggests that it could have used the Chicago, Grand Valley, or Fort Wayne outlets to gain access to glacial lakes in Ontario (Mandrak and Crossman 1992). Its discovery in 1972-1980 in the North Thames River (open circles in Figures 3 and 4) so far from other populations suggests that the species was introduced probably from bait buckets. Alternatively, recent natural dispersal from Michigan populations via Lake St. Clair and the Thames River is a distinct possibility. No barriers exist now or have existed in the past to prevent dispersal from Lake Saint Clair up to the North Thames River (Jack Robertson, Lower Thames Valley Conservation Authority, personal communication). Dispersal up the North Thames River would, however, been prevented after 1950–1952 when the Fanshawe dam was being constructed. Populations in the Niagara River, St. Clair River, and Essex county streams are closer to United States populations and it is more likely that these populations have resulted from natural dispersal. The Essex County records are 30–40 km from Michigan populations in Lake Erie tributaries. The St. Clair River records are about 35 km from records in Michigan tributaries of Lake St. Clair. The Niagara River records are located approximately 22 km northeast from specimens captured near the mouth of Eighteenmile Creek, draining into the south east end of Lake Erie, New York (Cornell University Catalogue number 20044). The Central Stoneroller has also been found in tributaries of the Niagara River in New York where it was recorded in several streams in the upper parts of Buffalo Creek from 1928 to 1949 (Greeley 1929, University of Michigan Museum of Zoology, and Cornell University collection records).

Underhill (1957) suggested that the presence of *Campostoma anomalum* in the upper Mississippi River above the St. Anthony's Falls in Minnesota is best explained by bait-bucket introduction. The Central Stoneroller has also been introduced into New Mexico (Burr 1980) and Connecticut (Nature Conservancy 1997). It has been suggested (McKee and Parker 1982; Litvak and Mandrak 1993) and it

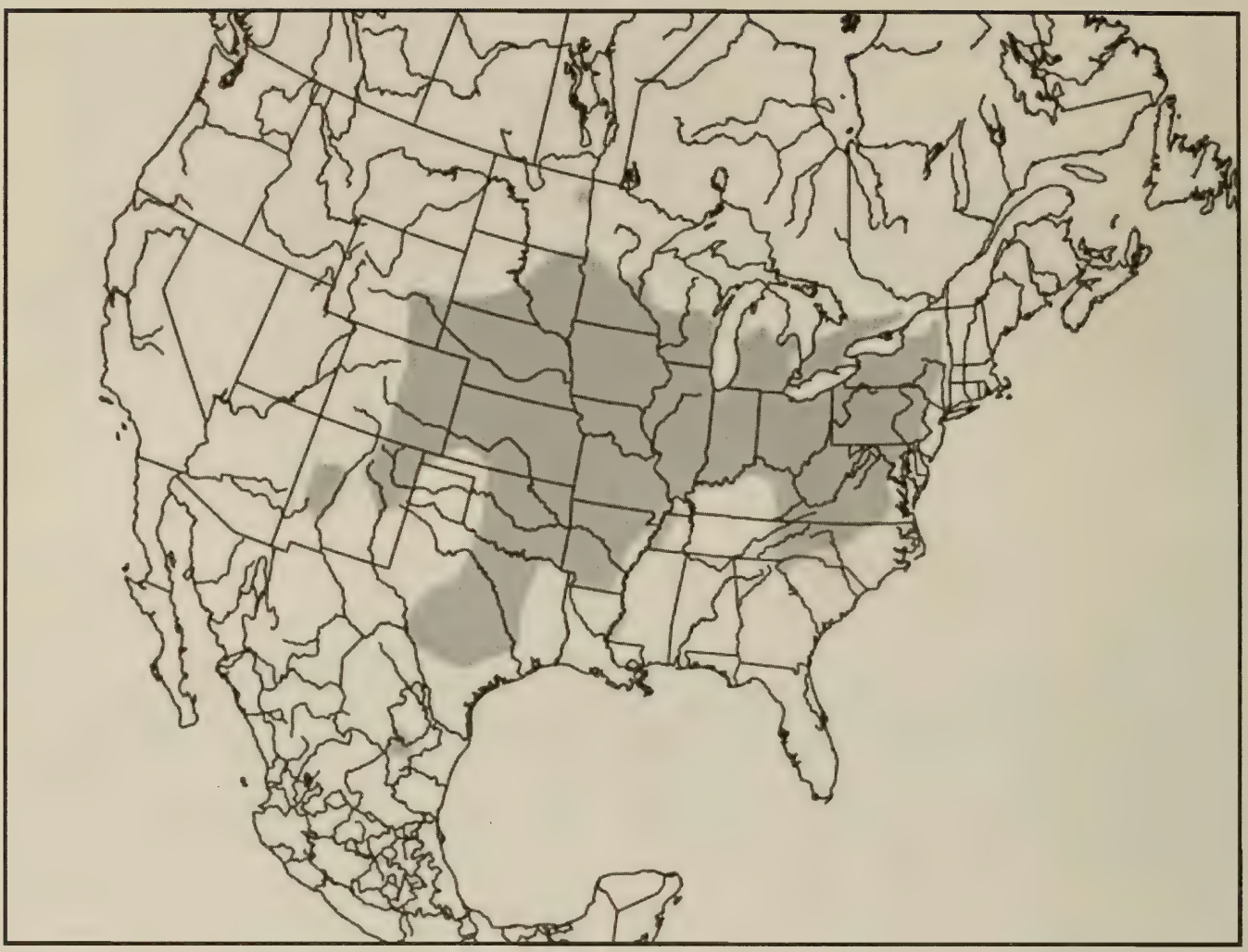

FIGURE 2. North American distribution of the Central Stoneroller. Adapted from Burr (1980) and Page and Burr (1991).

seems likely that some Ontario populations especially those in central and eastern Ontario have been introduced. It is considered to be one of the best bait species for bass (*Micropterus* spp.), Walleye (*Stizostedion vitreum*) and catfish (Ictaluridae) (McAllister 1987) and is known to be sold in Ottawa (Coad 1995), Toronto (Litvak and Mandrak 1993) and Parry Sound (E. McIntyre, OMNR, personal communication) to anglers who travel to a variety of places in southern Ontario.

Protection

The Federal Fisheries Act legislates against destruction of fish habitat but the existence of this legislation is not always successful in preventing this destruction.

Classified as a Vulnerable species in 1985, the Central Stoneroller may have received some proactive protection from adverse environmental impacts of new developments through the Ontario Planning Act. However, as a result of amendments to this Act in 1996, this protection now applies only to Threatened and Endangered species (Ian Buchanan, OMNR, personal communication). There are, however, fish habitat protection provisions in the new Planning Act (Alan Dextrase, OMNR, personal communication). The species is classified globally as G5 (very common) and in the United States it is classified as N5 (very common). Johnson (1987) listed the Central Stoneroller as Special Concern in North Dakota although its S-rank in that state is S4 (common) according to the Nature Conservancy (1997*). In Louisiana, it has an S-rank of S2 (very rare). It is considered common (S4) or very common (S5) in 22 states and its S-rank in five other states is unknown (Nature Conservancy 1997*).

Population Size and Trend

Although the Central Stoneroller is considered a very common fish in many parts of the United States (Pflieger 1975; Smith 1979; Trautman 1981; Cooper 1983; Page and Burr 1991; Nature Conservancy 1997*), it may be rare or declining in Louisiana (S2), North Dakota (S3) (Nature Conservancy 1997*) and Wyoming (Baxter and Stone 1995).

*See Documents Section

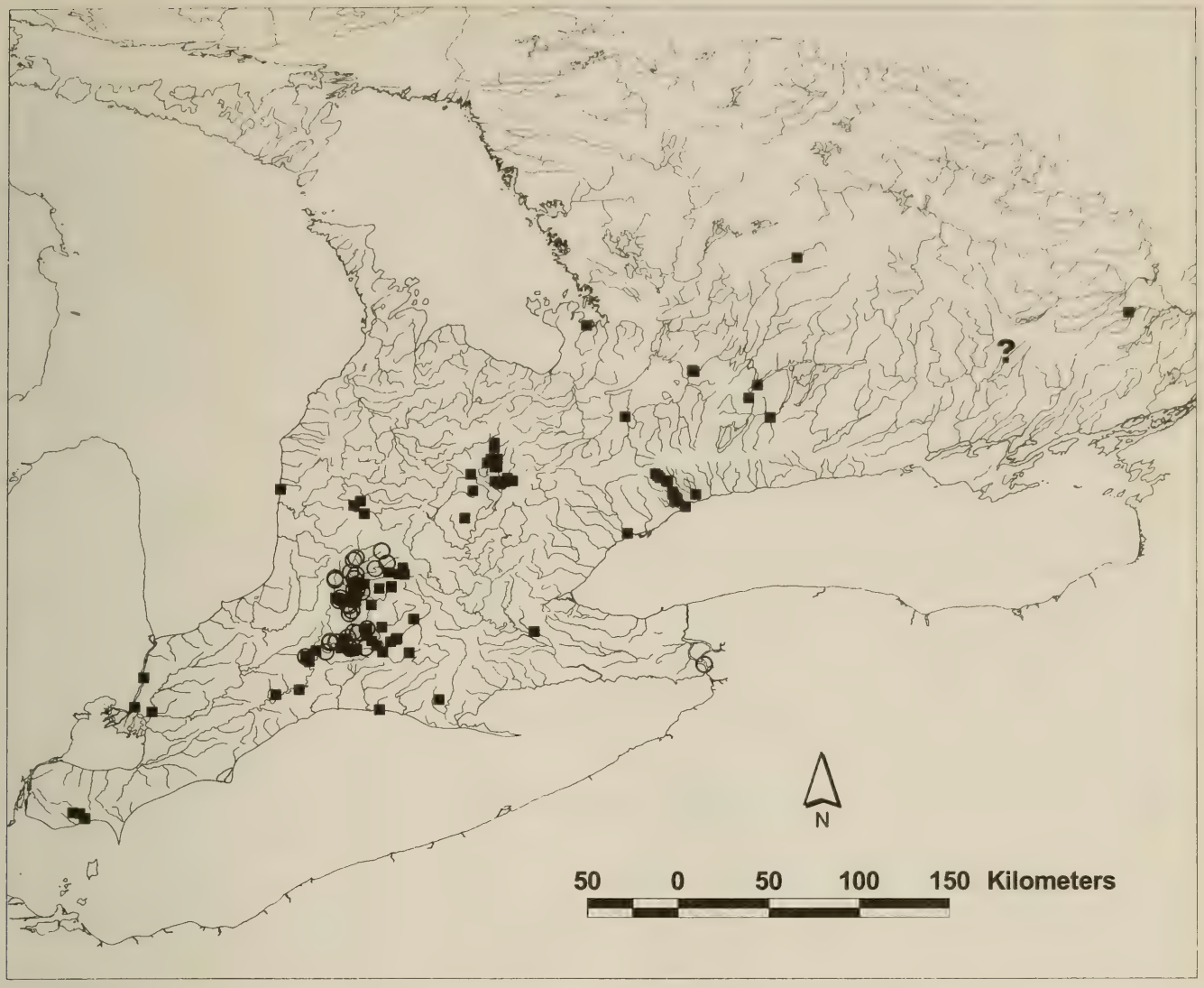

FIGURE 3. Canadian distribution of the Central Stoneroller, 1972 to 1996. Open circles represent records according to McAllister (1987). Solid squares represent records discovered since McAllister (1987). The question mark represents The Kaladar area collections.

McKee and Parker (1982) reported that it was frequently the most common fish in much of the upper Thames drainage. They gave density estimates for Ontario (0.37–3.72 fish m^{-2}, n = 3) that are similar to those given by Mundahl and Ingersoll (1989) for Ohio (0.10–3.91 fish m^{-2}) and other parts of the United States (0.07–3.1 fish m^{-2}). No population estimates have been conducted on Canadian populations. Based on relative abundance to other species in catches, the Central Stoneroller is moderately abundant in several of the streams outside the Thames drainage. It comprised 0.4 to 5.1% ($\bar{x} = 1.6$, n=7) of the number of specimens in collections made in the Rouge River system and represented 0.6 to 16.5% ($\bar{x} = 6.1\%$, n = 3) of the catch at the three collections made in 1996 in Essex County streams.

A 1993 electrofishing survey of upper Thames streams in Oxford County captured a total of 32 Central Stonerollers at 7 of 59 sites sampled (ROM Accessions 6087, 6090, and 6107). The species was abundant at one site where it represented 55% of 22 specimens captured and moderately abundant at two sites where it comprised 3 of 15 and 8 of 52 specimens.

A 1996 survey of creeks by the Grand River Conservation Authority discovered a well-established population of Central Stonerollers in the upper Grand River drainage near Grand Valley and Luther Lake. It was found at 14 of 30 sites sampled. A total of 215 *Campostoma anomalum* were captured which represented 6.4% of all specimens collected. At three sites there were more stonerollers caught than any other species and at another three sites it was the second most abundant species in the catches (Grand River Conservation Authority, unpublished data).

The cause of both the rapid increase in abundance and expansion of range in the Thames and subsequently in the rest of southern Ontario is unknown. McAllister (1987) speculated that habitat could have improved as the result of climatic conditions. It is also possible that removal of riparian vegetation and heavy use of fertilizers in the agricultural areas have

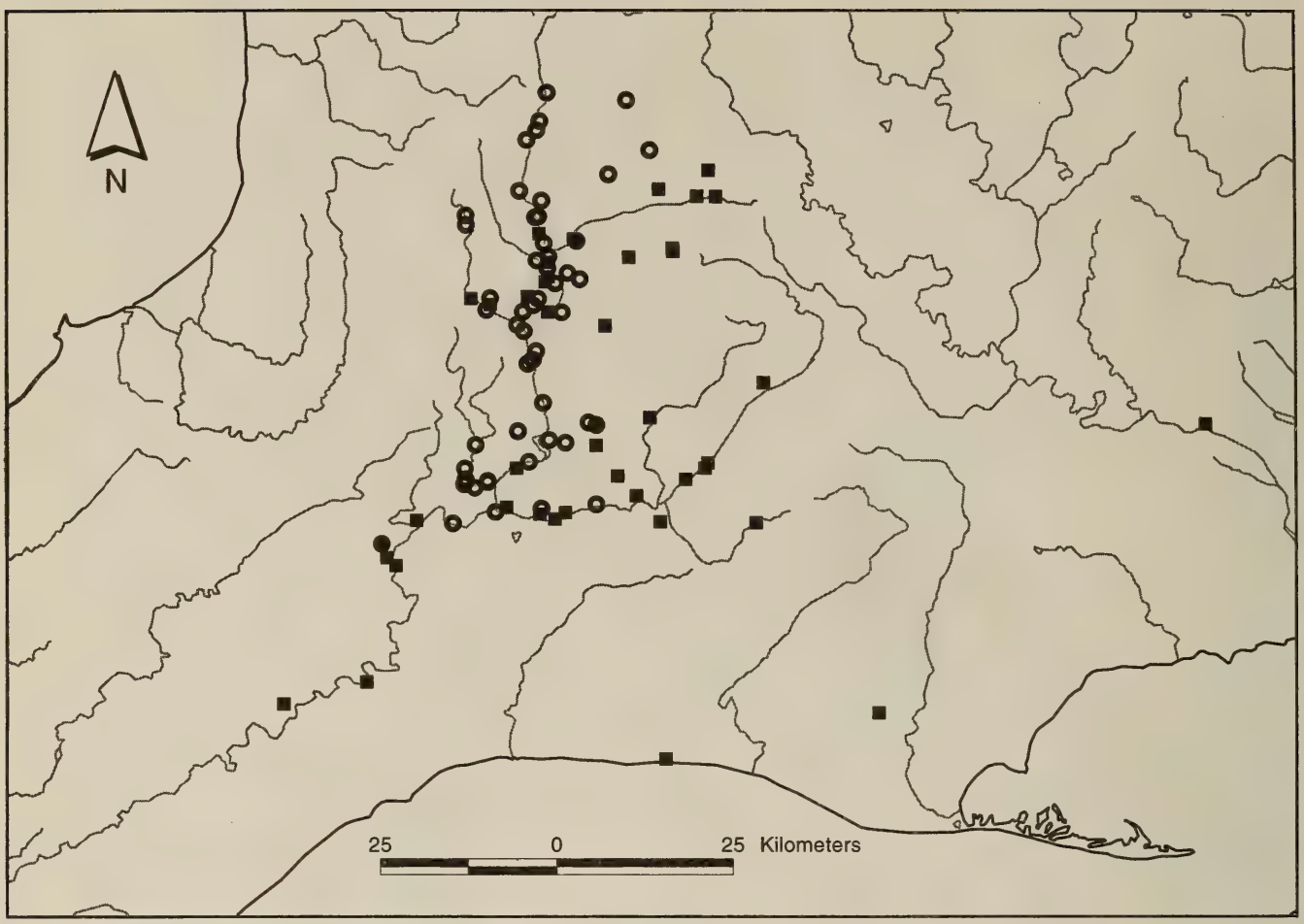

FIGURE 4. Distribution of the Central Stoneroller, 1972 to 1996 in the Thames River drainage. Open circles represent records according to McAllister (1987). Solid squares represent records discovered since McAllister (1987).

increased the food supply for *Campostoma anomalum*. A possible factor is increased awareness of fish collectors who have been more watchful for this species. However, the sudden appearance of the species in the North Thames in the 1970s does not appear to be the result of misidentification of the species in earlier collections. McKee and Parker (1982) noted that they found *Campostoma anomalum* abundant at many sites where they were not found by C. G. Gruchy in 1972. Collections were made in the North Thames drainage in 1936, 1946, 1953 and 1965 (ROM records). Specimens in the ROM collection, of species such as *Hybognathus hankinsoni, Nocomis* species, and *Rhinichthys atratulus* which could have been confused with *Campostoma*, were examined but no Central Stonerollers were found suggesting that the North Thames population resulted from a recent introduction followed by a rapid increase in abundance.

It is not known whether the two small specimens captured at the confluence of Frenchman's Creek and the Niagara River in 1977 represented strays from nearby American creeks or an established population. It is unlikely that the Central Stoneroller is established there now because surveys since 1977 have been unable to detect it. Sampling at that site conducted in 1979 by Parker and McKee (1980*), the OMNR (1979 surveys), and ROM in 1996 and 1997 have failed to capture any specimens.

Habitat

Although a few specimens have been captured in large rivers with little current, the Central Stoneroller thrives in small rivers and creeks of moderate gradient (0.5–41 m/km) where habitat consists of riffles and adjacent pools with rocky substrate. McKee and Parker (1982) indicated that it was found in North Thames streams with gradients of 1.0–3.7 m/km but was absent in the Thames River system where the gradient decreased abruptly to 0.5 m/km. In Little Rouge Creek, where the Central Stoneroller has been captured from its mouth to near its headwaters, average gradient is approximately 5 m/km. Average gradients vary from 2 to 6 m/km in Essex County streams. Lennon and Parker (1960) noted that the species was not present when gradients increased beyond 41m/km. Kraatz (1923) recorded a few specimens from lakes and it has also been recorded from one lake in Ontario.

Mundahl and Ingersoll (1989) noted that population densities of *Campostoma anomalum* in a small Ohio stream were found to be higher in pools and

TABLE 2. New locations in Canada for *Campostoma anomalum* since previous status report (McAllister 1987).

Location	Year	Source of Record
Mill Creek in Kingsville	1978	ROM 35374, OMNR: Ward and Patterson
Creek in village of Bogies Beach	1980	ROM 41606, OMNR: Maronets and Groom
Rouge River, Metro Toronto	1984	ROM Accession 4749: Holm and Boehm
Deer Creek, Norfolk County	1984	ROM 57374, OMNR: Colonello
North Sydenham River	1984	ROM 46164 Boehm, MacCulloch, Holm
Kaladar area	1986	NMC 86-0206, NMC89-0206, NMC89-116
Lower Grand River	1986	T. Warren, SSFC
Talbot River, Lake Simcoe	1987	ROM 57984, OMNR: Shackleton, Ross, Galamb
Scugog River, Sturgeon Lake	1988	T. Warren, SSFC
Duffins Creek, Metro Toronto	1989	ROM 56735 U of Toronto: Wichert and Regier
Thames River at Tate's Bridge	1989	ROM 56950 ROM fieldwork: Holm et al.
Wye River	1990	ROM 59416 Boehm
Humber River, Metro Toronto	1992	ROM 64776 RSMI Consultants: Boyd
St. Clair River	1993	ROM 67799 OMNR: Long and Masterson
Sally's Creek, Woodstock	1993	ROM Acc. 6087 OMNR Aylmer: Schraeder
Upper Maitland River drainage	1995	MNR: Malhiot 1996*
Carroll Creek, upper Grand River	1995	ROM 70160 U of Waterloo: Fitzgerald
Tay River tributary, SW of Perth	1995	ROM 69106 Beak Consultants: Meisenheimer
Upper Grand River near Luther Lake	1996	ROM 70501-70511: Grand River Conservation Authority
St. Clair River, Baby's Point	1996	ROM 70496, ROM: Holm, Ramshaw, Guppy
Wigle Creek, 5 km NW of Kingsville	1996	ROM 70396, ROM: Holm, Ramshaw, Guppy
Cedar Creek, 8 km NW of Kingsville	1996	ROM 70393, ROM: Holm, Ramshaw, Guppy
Stothart Creek Haliburton County	1996	M. Brohm, SSFC†
Silver Creek, 13 km S of Aylmer	1996	G. Colgan, SSFC†
Wilson Creek, Lake Simcoe	1996	K. Good, SSFC†
Pigeon River, 5 km SW of Omemee	1996	A. Gibson, SSFC†

†Via T. Warren Sir Sanford Fleming College (SSFC)

riffles with areas of open canopy, probably due to the higher primary productivity and therefore increased food supply.

Campostoma anomalum appears to be a hardy species that can tolerate a wide range of environmental conditions. It is frequently found in urban or agricultural locations with an assemblage of widespread and common species which are tolerant of high levels of turbidity, contaminants and extreme fluctuations in flow. The species has been described as being both "intolerant of silt" (Smith 1979) and "tolerant of turbid, silty waters" (Burr 1980). McAllister (1987) documented that the species can tolerate oxygen levels as low as 3 mg/l and fluctuating turbidity levels in the North Thames River.

Descriptions of bottom type for 42 ROM records indicate that the Central Stoneroller is found primarily in creeks and rivers that have some rocky components (80%) such as boulder, rubble, or gravel and less frequently (20%) over bottoms consisting of only one or more of clay, silt, sand, detritus, and muck. In 20 of the records that had a comment on vegetation 14 (70%) had some sort of aquatic vegetation (usually submerged) and six recorded "NONE". Of 37 records with notes on water current, only two of the streams (6%) had no flow, the remainder had at least a slight current. Nine (36%) of 25 locations had turbid water (secchi less than or equal to 0.5 m). Stream widths ranged from 3 to 60 m ($\bar{x}$ = 23 m, n = 15).

A study (OMNR), conducted on municipal drains in the drainages of the North Thames and Maitland rivers, found *Campostoma anomalum* in streams with widths of 0.7–3.5 m ($\bar{x}$ = 2.1), depth of water 6–30 cm ($\bar{x}$ = 15.4), water flows of 19–757 litres·minute^{-1} ($\bar{x}$ = 185), and temperatures up to 25°C ($\bar{x}$ = 17.4). Bottoms consisted primarily of gravel ($\bar{x}$ = 29%), rubble ($\bar{x}$ = 27%), boulder ($\bar{x}$ = 18%) and sand ($\bar{x}$ = 13%) with minor components of silt ($\bar{x}$ = 7%), marl ($\bar{x}$ = 3%) and rarely clay ($\bar{x}$ = 1%) (Malhiot 1996*).

Habitat data was collected for the Upper Grand River collections in late August 1996 by the Grand River Conservation Authority (ROM Accession 6456). Central Stonerollers were found in streams with an average width of 1.7–24 m ($\bar{x}$ = 8 m) and average depths of 12–42 cm ($\bar{x}$ = 24). Water temperatures varied from 18 to 23°C averaging 3°C lower than air temperature. Dissolved oxygen was 7.4–9.1 mg·l^{-1} ($\bar{x}$ = 8.2), pH was 8–9 ($\bar{x}$ = 8.2) and conductivity was 230–500 μ mhas ($\bar{x}$ = 366). Aquatic macrophytes were usually present at the sites. The greatest number of Central Stonerollers (81) was captured at a site where the land use and terrestrial vegetation was described as follows: "cattle grazing — cattle access to stream — no buffer — severe erosion along banks". Many of

the other sites where Central Stonerollers were captured, were developed for residential and agricultural uses with some natural shoreline, meadow or woods. Bottom was primarily rocky: bedrock (0–40%, $\bar{x}$ = 4.5), boulder (0–20%, $\bar{x}$ = 6.7), rubble (0–75%, $\bar{x}$ = 37.3), gravel (1–40%, $\bar{x}$ = 17), sand (3–20%, $\bar{x}$ = 16.4), silt (0–10%, $\bar{x}$ = 4.5), clay (0–10%, $\bar{x}$ = 0.9), muck (0–40%, $\bar{x}$ = 6.0) and detritus (0–60%, $\bar{x}$ = 6.8). A comparison of the 13 sites where *Campostoma anomalum* occurred with 14 sites where it was not captured in the upper Grand River indicated that the species was found more frequently on rocky, larger sized substrates (bedrock to gravel) than soft and smaller-sized substrates (sand, silt, clay, muck and detritus). The species also occurred at sites which were more open and had more riffles and pools.

Small-sized gravel and nearby pools are necessary for spawning. Spawning areas in Missouri are often so shallow that the backs of males are exposed during pit construction (Pflieger 1975).

Biology

See McAllister (1987) for information on reproductive capability and age. Updated information on species movement and diet is summarized below.

Species Movement

The movements and migration of Canadian populations of the Central Stoneroller have not been studied. Lennon and Parker (1960) found relatively little movement occurring in the Great Smoky Mountains National Park population. Miller (1962) cited three studies which indicated that this species migrated to spawn but found that one New York population had localized spawning migrations confined to movements from pools to adjacent riffles. He suggested that the length and duration of migrations depend on habitat suitability. A study of the movements and home range of the species in a stream in Ohio in early fall indicated that the species had a small home range, averaging 35 ± 14.1 m ($\bar{x}$ ± 95% CI), and moved a maximum of 135 m (Mundahl and Ingersoll 1989). Rakocinski (1984) suggested that *Campostoma anomalum pullum* migrates upstream to spawn in a creek in Illinois. Mundahl and Ingersoll (1989) suggested that more examination is needed to determine if the species exhibits a true spawning migration, and if so, whether the fish return to their original home ranges following spawning. They also suggested that predators such as bass and large Creek Chub (*Semotilus atromaculatus*) will restrict movements of *Campostoma* and limit the home range size. Predators also influence emigration of stonerollers from pools (Matthews et al. 1987).

Diet

The Central Stoneroller is known for being highly herbivorous, feeding almost exclusively on periphyton. Inorganic matter such as sand and silt can account for up to 75% of the gut contents of adults. It is not known if the inorganic material is ingested accidentally while scraping attached algae or intentionally to help grind algal cells like stones in a bird's gizzard. Small percentages of macroinvertebrates (primarily chironomids) are also reported in dietary studies of the Central Stoneroller. Johnson and Dropkin (1992) found that this species would feed on larval American shad (*Alosa sapidissima*) in a situation where the shad were abnormally high in abundance. Kraatz (1923) found that diatoms, particularly *Navicula* and *Nitzschia*, were prominent in the diet of Central Stonerollers in Ohio. Other prominent food items were filamentous green algae such as *Spirogyra*. Small young had consumed not only a high percentage of diatoms but significant portions of zooplankton such as rotifers, copepods, and cladocera. They also consumed less inorganic matter (15–25%), which may be a reflection of a lesser amount of bottom feeding. In a small stream in the Ozarks in northeastern Oklahoma, *Campostoma anomalum* showed little seasonal variation in diet. Gut contents consisted of 38% non-filamentous algae, 28% sand, 21% detritus, 7% filamentous algae, 3% vascular plants, and 3% macroinvertebrates of which most were chironomids (McNeeley 1987). Fowler and Taber (1985) found that *Campostoma anomalum* in Missouri fed during daylight consuming 27% of their body weight per day. Foreguts contained detritus, diatoms (preferring non-motile over motile), inorganic matter and green and blue-green algae. McKee and Parker (1982) found that specimens from the North Thames drainage, Ontario, had 23% filamentous green algae with most of the remainder being inorganic material.

Limiting Factors

Potential limiting factors include availability of periphyton, excessive siltation and pollutants (McAllister 1987). Impoundment and channelization of streams has reduced its abundance in Virginia (Jenkins and Burkhead 1994) and Ontario (McAllister 1987; McKee and Parker 1982). The species appears to be moderately tolerant to siltation and turbidity but the species is generally found most often on rocky bottoms where the current has swept away silt. It seems to actively avoid clay bottoms which may explain why it has not shown up in Frenchman's Creek since 1977. It will utilize sections of streams which dry up later in the summer in Illinois (Rakocinski 1984). Cold temperatures are probably not limiting because it has spawned in water as low as 11°C (Jenkins and Burkhead 1994).

The commonly encountered black spot parasite (*Uvulifer* sp.) has been shown to adversely affect some species of fishes through increased mortality, reduction in weight gain, low condition coefficient and slow growth. McKee and Parker (1982) noted that most of the specimens they collected were infected with black spot, sometimes heavily.

However, this is likely not a limiting factor for the species as Baker and Bulow (1985) demonstrated that the condition of Central Stonerollers was not adversely affected by parasite density. Even heavily infected individuals appeared healthy in a central Tennessee stream.

Besides piscivorous fishes such as bass, the Central Stoneroller is preyed upon by avian predators such as the Belted Kingfisher (*Ceryle alcyon*) and the Great Blue Heron (*Ardea herodias*). The Belted Kingfisher preferred *Campostoma anomalum* over other more common smaller minnows in one New York study (cited in Matthews et al. 1986). Central Stonerollers would be particularly susceptible to terrestrial predators during the spawning season when they occur in shallow riffles. Both the Belted Kingfisher and the Great Blue Heron are common summer residents in Ontario (James 1991). The Mink (*Mustela vison*), common in Ontario (Dobbyn 1994), is also a potential predator (Hamilton 1959).

Special Significance of the Species

Much has been written recently on the important ecological role played by *Campostoma anomalum* in the aquatic ecosystem. Sometimes referred to as a "stream cow", it uses a resource (algae, periphyton) not commonly exploited by other species of Canadian fishes, converting the primary productivity of the stream into a form that can be used by piscivorous fishes and terrestrial predators such as kingfishers, herons and mink. Where abundant, it has a significant effect on the standing crop of algae in streams and the composition of the algal community. In field experiments in Oklahoma, after *Campostoma anomalum* was introduced into streams, the dominant algal overstory such as filamentous green algae (*Spirogyra*) was replaced with a faster-growing community of low-growth forms of diatoms (*Navicula, Achnanthes, Gomphonema, Cymbella, Tabellaria, Fragilaria, Synedra, Cocconeis, Melosira*) and blue-green algae (mostly *Oscillatoria*) (Gelwick and Matthews 1992).

Invertebrate and bacteria populations are also affected. Through faecal production and mechanical fragmentation, the Central Stoneroller alters the size of the particulate organic matter in the sediment creating a detrital food resource that is preferred by certain types of invertebrates and bacteria. On the other hand, by reducing the algal overstory other types of invertebrates lose their cover and food source. In Oklahoma, non-tanypodine chironomids such as *Dicrotendipes* and *Stictochironemus* increased in grazed areas whereas amphipods (*Hyalella azteca*) decreased as the result of stoneroller grazing (Gelwick and Matthews 1992). Vaughn et al. (1993) demonstrated negative impacts of *Campostoma* grazing on crayfish (*Orconectes*) and beneficial effects on snails (*Physella*). Growth of crayfish was reduced by the removal of their food source, the dominant algal overstory, and by prevention of day-time feeding of the crayfish. Snails grew larger and delayed reproduction because grazing by *Campostoma* increased food available to the snails by making low growth forms of periphyton more accessible and increasing the bacteria in the sediment.

Bacteria play a key role in nutrient cycling, conversion of non-living organic carbon into biomass and as a food source for invertebrates (Findley et al. 1986). By altering sediment particle size and removing the algal overstory, *Campostoma anomalum* also affect bacteria populations both positively and negatively. Bacteria associated with the healthy algal overstory declined in grazed areas (Gelwick and Matthews 1992). Gardner (1993) conducted experiments on artificial streams and found that grazed streams resulted in a higher proportion of fine benthic particulate organic matter (41–156 µm) than the proportion in ungrazed streams. He suggested that this particle size alteration would result in increased bacterial activity and biomass in the sediment.

Limited evidence suggests that high densities of *Campostoma* lowers diversity of small fishes, but *Campostoma* appears to improve feeding opportunities of some species by displacing invertebrates from the bottom making them more available to insectivores (Matthews et al. 1987).

Eddy and Underhill (1974) attributed little value to this species as a bait minnow and as a forage fish in Minnesota. However, it is important as a bait fish and sometimes preferred over trout as a food fish by fishermen in Virginia and Tennessee (Jenkins and Burkhead 1994). In Ontario, Litvak and Mandrak (1993) found it ranked 18 of 28 in frequency of occurrence in Toronto bait dealers' tanks, just ahead of the Emerald Shiner. Coad (1995) also reported that the species is excellent bait and is sold by bait dealers in Ottawa which get them from a source in south central Ontario.

Lennon and Parker (1960) showed that in Smoky Mountains National Park the Central Stoneroller can reduce numbers of Rainbow Trout (*Oncorhynchus mykiss*). It spawns in spring just after the trout and its activities destroy the redds before the trout eggs hatch. In Ontario streams, this would have an impact on the introduced Rainbow Trout but would not affect fall spawners such as the introduced Brown Trout (*Salmo trutta*), and Pacific salmons (*Oncorhynchus* spp.) and the native Brook Trout (*Salvelinus fontinalis*).

Evaluation

The Central Stoneroller is undergoing a range expansion and should no longer be considered in jeopardy in Canada. The number of new records has more than quadrupled since the 36 records documented by Parker and McKee (1980*). The species appears to have become established in many waters

of Ontario as a result of a combination of bait-bucket introductions and natural dispersal.

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Notes

Common Raven, *Corvus corax*, Observed Taking an Egg from a Common Loon, *Gavia immer*, Nest

ROBERT ALVO[1] and PETER J. BLANCHER[2]

[1]GAVIA Biological Services, 58, rue des Parulines, Hull, Québec J9A 1Z2, Canada
[2]Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Blvd, Hull, Québec K1A 0H3, Canada

Alvo, Robert, and Peter J. Blancher. 2001. Common Raven, *Corvus corax,* observed taking an egg from a Common Loon, *Gavia immer* nest. Canadian Field-Naturalist 115(1): 168–169.

We report an incident of a Common Raven (*Corvus corax*) taking an egg from an active Common Loon (*Gavia immer*) nest, and two other possible similar events. The fact that ravens can take whole eggs, leaving no trace of eggs on the nest, could explain a considerable proportion of the missing loon eggs that researchers have documented, particularly on lakes with few humans.

Key Words: Common Loon, *Gavia immer*, Common Raven, *Corvus corax*, egg, nest, predation.

Predation by Common Ravens (*Corvus corax*) on eggs can be a serious problem for waterfowl management in some places (Braun et al. 1978). Ravens can also remove considerable numbers of eggs from the nests of colonial aquatic birds such as gulls, murres and cormorants, concealing for future use what they cannot eat at once (Bent 1946). Montevecchi (1978) reported ravens frequently supplanting nesting Black-legged Kittiwakes (*Rissa tridactyla*) by suddenly approaching them closely while calling loudly, or by physically attacking them. He also watched a raven displace a kittiwake from a nest by pulling a tuft of dried grass from sod on a cliff face and dropping it on the kittiwake – the raven then jumped down and rummaged through the empty nest.

Loons generally nest within 1-2 m of a freshwater pond, tarn or lake. Their eggs are susceptible to predation from mammalian and avian predators. Known or suspected avian egg predators of the five loon species include Common Ravens, American Crows (*Corvus brachyrhynchos*), Hooded Crows (*C. corone*), Glaucous Gulls (*Larus hyperboreus*), Herring Gulls (*L. argentatus*), Great Black-backed Gulls (*L. marinus*), Lesser Black-backed Gulls (*L. fuscus*), Parasitic Jaegers (*Stercorarius parasiticus*), Long-tailed Jaegers (*S. longicaudus*), Sandhill Cranes (*Grus canadensis*), and Snowy Owls (*Nyctea scandiaca*). McIntyre (1977) and Titus and VanDruff (1981) have reported American Crows eating and/or puncturing loon eggs. No one has reported seeing Common Ravens taking loon eggs. However, Common Loon eggshell fragments were found in a raven's nest (Titus and VanDruff 1981).

Here we report an incident of a raven taking a Common Loon egg from an active nest, and two other possible similar events. Each incident occurred in a different loon territory in or adjacent to Killarney Provincial Park (46°06′N, 81°13′W), southwest of Sudbury, Ontario, in 1981 and 1982 during a study of the effects of acid precipitation on avian breeding success.

In the first territory, in a stump-filled bay at the east end of Johnnie Lake (46°05′45″ N, 81°12′45″ W), PB discovered a loon nest with one egg 14 May 1981. The nest was on a mud platform in the centre of this large area of water, stumps and *Myrica gale* shrubs. On 23 May and 27 May, a loon was incubating one egg, and a loon was incubating again on 30 May. On 3 June, as a loon incubated, a raven flew directly toward the nest from the direction of the main portion of the lake. The loon slipped off the nest without any resistance or sound as the raven approached, landed, picked up the egg whole and flew back toward the main part of the lake. Meanwhile, the loon swam several hundred metres toward the main part of the lake and joined a second loon, after which one gave a few long wails, then both flew away. No loons were observed on this territory on 7 June or 10 June, but a pair was seen on 14 June. A loon was incubating a new nest with two eggs in the same stump-filled bay on 28 June. A loon was incubating on 12 July and 15 July, and on 19 July a pair with two chicks was seen in the bay.

In the second territory, on 29 May a loon was incubating in a stump-filled bay at the west end of Johnnie Lake (46°05′00″ N, 81°14′45″ W), approximately 3 km southwest of the first territory. The

number of eggs was not determined. The nest had disappeared by 5 June, but a loon pair was seen at the entrance to the bay. One loon was seen very close to the old nest site on 9 June. On 13 June, a raven flew up from a small grass island about 100 m west of the first nest with what appeared to be a loon egg. The loon pair nearby in the water was silent. Upon inspection of the island, PB found an empty loon nest in good condition where the raven had been. On 17 June, a loon was incubating in a new nest at the site of the initial nest. Incubation of an unknown number of eggs was observed on 21 June, 25 June, 29 June, 2 July, 6 July and 10 July, despite the presence of ravens in the bay on 2 July and 10 July. The nest was empty on 15 July, and contained no eggshells. However, a single loon chick, young enough to be from this nest, was seen with its parents on 20 July, 23 July, 30 July and 9 August near the entrance to the bay.

The third territory was in the north bay of Ruth-Roy Lake (46°05′30″ N, 81°15′00″ W), a fishless, acidic (pH 4.5) lake. A loon pair was seen on 15 May 1982 near what was apparently a nest in construction on the north side of a small island. The nest contained no eggs on 25 May, but a single loon was seen close by. A pair was seen near the nest on 29 May, and incubation was observed on 5 and 9 June. The number of eggs was not determined. On 13 and 17 June, the nest was empty and no loons were observed. On 21 June, on the west side of the lake's north section (ca. 400 m from the first nest) a raven flew up from the back of a stump with something large in its bill, which could have been a loon egg, and flew directly away from PB while a pair of Eastern Kingbirds (*Tyrannus tyrannus*) attacked it (a nearby kingbird nest had lost 3 of 4 eggs since 17 June). A nearby loon uttered low, quiet wail-like "moaning" calls. Inspection of the stump from which the raven had flown revealed a loon nest with one intact egg. On 25 June, the loon and kingbird nests were both empty and no loons were seen. The lake was visited nine times from 25 June to 27 July, and the only loon sighting was on 15 July, when a pair was seen in the lake centre before flying off.

It is clear that Common Ravens are loon nest predators, and it is now known that ravens may displace loons from their nests to take an egg, as they do to other birds. However, it is not clear to what extent this activity decreases loon breeding success, because the loons may renest successfully. In Wyoming, raven home ranges varied from 6.7 to 10.9 km^2, which means that an individual could travel up to 3 km or more (Roy and Bombardier 1996). All three loon territories were within 2 km of the site of a single raven nest in at least one year of the study, so it is possible that a single raven or raven family was responsible for all incidents reported here.

The fact that ravens may remove whole loon eggs from nests is a critical point to bear in mind during loon breeding surveys. We suspect that many nests found empty after having previously been found with eggs in the Sudbury area (RA, personal observations) were also the work of ravens.

We consider the observations presented here to be very fortuitous because it is rare to observe such predation events. During a three-year study of loon breeding success, RA never observed any predation events on loon nests, but he found numerous depredated nests (Alvo et al. 1988).

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Two Cases of Infanticide in a Red Fox, *Vulpes vulpes*, Family in Southern Ontario

VALERIA VERGARA

Trent University, Biology Department, Peterborough, Ontario K9H 7B8, Canada

Vergara, Valeria. 2000. Two cases of infanticide in a Red Fox, *Vulpes vulpes*, family in southern Ontario. Canadian Field-Naturalist 115(1): 170–173.

Two cases of directly observed infanticide in a Red Fox (*Vulpes vulpes*) family in southern Ontario are described. These observations were made in the context of a natal den study that was aimed at comparing male and female parental roles in wild Red Foxes.

Key Words: Red Fox, *Vulpes vulpes*, infanticide, parental care, intraspecific predation, offspring mortality, Ontario.

Infanticide is commonly defined as the killing of dependent young by a conspecific (e.g., Fosey 1984; Hayssen 1984; Hrdy 1979; vom Saal 1984). Infanticide in mammals may be followed by cannibalism (Brooks 1984). This process of both killing and eating an individual of the same species is known as intraspecific predation (Polis 1981). In mammals, intraspecific predation involves adults preying on immature animals and cubs (i.e., infanticide) more often than adults preying on other adults (Polis 1981).

Many descriptions of infanticide in mammals have been published (e.g., Brown Bears, *Ursus actos*: Olson 1993; Alpine Marmots, *Marmota marmota*: Coulon et al. 1995; Hanuman Langurs, *Presbytis entellus*: Borries 1997; Ground Squirrels, *Spermophilus beecheyi*: Trulio 1996; Hippopotamus, *Hyppopotamus amphibius*: Lewison 1998). In canid species, infanticide has occasionally been reported. Camenzind (1978) presents circumstantial evidence of infanticide in Coyotes, *Canis latrans*, by trespassing conspecifics. Maternal infanticide has been studied in captive Silver Foxes, *Vulpes vulpes* (Braastad and Bakken 1993). However, I know of no specific example of infanticide in wild Red Foxes (*Vulpes vulpes*). I describe here two cases of directly observed infanticide in a Red Fox family, witnessed during a natal den study of eight Red Fox families aimed at comparing parental roles in male and female Red Foxes in southern Ontario (Vergara 1996).

The fox family consisted of a large litter of nine kits, an adult female, and an adult male. I observed this family for a total of 131 hours, from 6 May, 1995 (nine kits, 6 weeks old) to 6 June, 1995 (five kits, 10 1/2 weeks old). Two dens, 18 m apart, both with multiple entrances, were in use simultaneously by this family. The whole den area (encompassing both dens with their multiple entrances) was located in the middle of a hay field, 50 m from a farm house, and was easily observed from the kitchen window (location: 20 km to the north-west of Bobcaygeon, Verulam Township, Victoria County: 44°33′, 78°40′). The driveway to the farmhouse separated the hay field from a cow pasture.

On 8 May 1995, the adult female arrived at 1942 h carrying a small-size rodent that she fed to one of the kits. She nursed the kits for 2 minutes, then disengaged herself and trotted 25 m away from the den mound. The kits became very active. Some followed the female and began exploring the pasture, while others were involved in energetic play-chasing over the field where both dens were located. At 1950 h something frightened the female, who left the den site at a fast run, and was soon out of sight. Some kits went back to the den mound, and others remained relatively far from it (20–30 m), exploring and playing. At 1953 h an adult Red Fox of unknown sex and age, never recorded before, came trotting toward the den. It adopted an aggressive posture when it passed by the den with its back arched and head and neck low. It snarled at one kit, which crouched down flattening its ears and then went underground. The stranger continued trotting towards the driveway where a single kit was sniffing around. The stranger immediately resumed its threatening posture, stalked the kit very briefly, dashed towards it, grabbed it by the neck and shook the kit vigorously. It then scurried away carrying the limp body of the kit in its mouth. The remainder of the litter stayed inside the den until dark.

Only 3 days later, on 11 May 1995, I recorded a very similar event. At 2100 h the light had faded almost entirely. I used the ambient light image intensifier scope, which allowed to view the immediate den area since this was also dimly illuminated by the light coming from the farm house. The kits (now only seven, one lost to infanticide and one lost to unknown causes) were alone, outside the den, not too active, and not ranging from the den mound. At 2110 h an adult fox of unknown sex and age came to the den. The kits crouched down instead of running out to greet the fox, which suggested that the animal was a stranger. This was corroborated by the fox's strange behaviour: it was running around with a very aggressive body posture (i.e. its back arched, its head and neck lowered). It grabbed a kit by the neck and shook it quite vigorously for a few seconds, as the remaining kits went in the den. It dropped the body

of the kit when the adult female arrived and chased the stranger away. When I ended my observation session at 2120 h, no Fox was visible outside the den. The next day I counted only 6 kits, one less than the previous day, which suggests that the stranger had indeed killed the kit before the female chased it away. I surveyed the den area but did not find the carcass of the kit.

The two cases of infanticide described above occurred in a litter that had a low male visitation rate, and was left unattended 80% of the time. During the 4 weeks that I observed this family, I only saw the adult male 8 times, compared to 42 visits from the vixen. The male brought food but interacted little with the kits: he never groomed them, played, or laid down with them, behaviors that were observed in the males of my other study families (see Vergara 1996 for details). His visits lasted between 4 and 8 minutes, about half to two thirds the length of the visits by the males in my other study families (Vergara 1996).

This low male den attendance may be consequential, particularly when we take into account that vigilant males spent most of their time at the den site (78 % on average) in the absence of the female. This is referred to as "pupsitting" or "den guarding" in other studies (e.g., Moehlman 1983, for Silverbacked and Golden Jackals, *Canis mesomelas* and *Canis aureus*; Malcom and Marten 1982, for African Wild Dogs, *Lycaon pictus*). Pupsitting may help to detect danger such as Humans, Coyotes or strange foxes. This grants the speculation the fewer and shorter male visitations to the den site in this particular family may have had some influence on the vulnerability of this litter to dangers such as infanticide, a possibility that needs testing, and invites further study. Activities away from the den may also be important forms of indirect care that would go unobserved in this den-centered study. Nonetheless, a male that is patrolling the boundaries of the territory may miss an intruder at the den site, especially considering the reported large size of fox farmland territories in Ontario (900 ha on average, Voigt and Macdonald 1984).

The phenomenon of killing of young by conspecific strangers, parents and siblings has been widely discussed in the context of a number of hypotheses (for review, see Parmigiani and vom Saal 1994). Most of them agree on the fact that the fitness of the killer is benefited. One of the possible immediate benefits of infanticide may be a nutritional one (Lüps and Roper 1990). In the present case, I do not know if the infanticidal Fox ate the kits that it killed (i.e. if it was a predatory act). However, this is not an unlikely possibility, as Red Foxes do eat conspecific carcasses. I observed fox kits feeding on their dead littermates in two of my study families (see Vergara 1996).

The significance of the observations reported here rests on the important role that infanticide could play in the dynamics of Red Fox populations. There are reports of intraspecific predation on immature animals or cubs substantially reducing populations of various species of carnivore (see Polis 1981 for extensive review). For example, adult Arctic Foxes, *Alopex lagopus*, may kill and eat other adults or pups during periods of low food availability, and this may be a factor in Arctic Fox population regulation (Chesemore 1975). Den-site behavioral studies would help to determine if infanticide in Red Foxes is more than incidental, and the degree to which it affects reproductive success. Only then we could start evaluating hypotheses addressing the adaptive basis and the significance of this behavior.

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An Unusual Record of a White-tailed Deer, *Odocoileus virginianus*, in the Northwest Territories

ALASDAIR M. VEITCH

Department of Resources, Wildlife & Economic Development, Government of the Northwest Territories, P.O. Box 130, Norman Wells, Northwest Territories, X0E 0V0, Canada.

Veitch, Alasdair M. 2001. An unusual record of a White-tailed Deer, *Odocoileus virginianus*, in the Northwest Territories. Canadian Field-Naturalist 115(1): 172–175.

The most northern record of White-tailed Deer (*Odocoileus virginianus*), approximately 100 km south of the Arctic Circle in the Northwest Territories (N.W.T.), is described. This and other observations from the N.W.T. and southeastern Yukon extend the known northern limit for White-tailed Deer in North America.

Key Words: White-tailed Deer, *Odocoileus virginianus*, range, Northwest Territories, Yukon, Arctic, parasite, global warming.

White-tailed Deer, *Odocoileus virginianus*, are the most important big game species in North America (Banfield 1977; Halls 1978) and have proven adaptable across their range (Hesselton and Hesselton 1982). The range of White-tailed Deer in Canada includes all provinces except the island of Newfoundland and Prince Edward Island. Most range maps and descriptions do not include either the Northwest Territories (N.W.T) or the Yukon Territory (e.g., Rue 1968; Banfield 1977; Whitaker 1980; Hesselton and Hesselton 1982). However, the first published sightings of White-tailed Deer in the N.W.T. were by from 1965–1966 in the southern Fort Smith-Wood Buffalo National Park area near the Alberta-N.W.T. border (Kuyt 1966). The earliest and most northern record of White-tailed Deer was from a hunter that killed 4 of 9 Deer at Little Doctor Lake west of Fort Simpson (ca. 61°55′N; 123°30′W; Figure 1) in 1959 or 1960 (Scotter 1974). Wishart (1984) documented expansion of this species in northern Alberta and in western and northern British Columbia. More recently, Gainer (1995) provided additional records in British Columbia and the southern N.W.T. from Fort Simpson to north of Great Slave Lake (Figure 1).

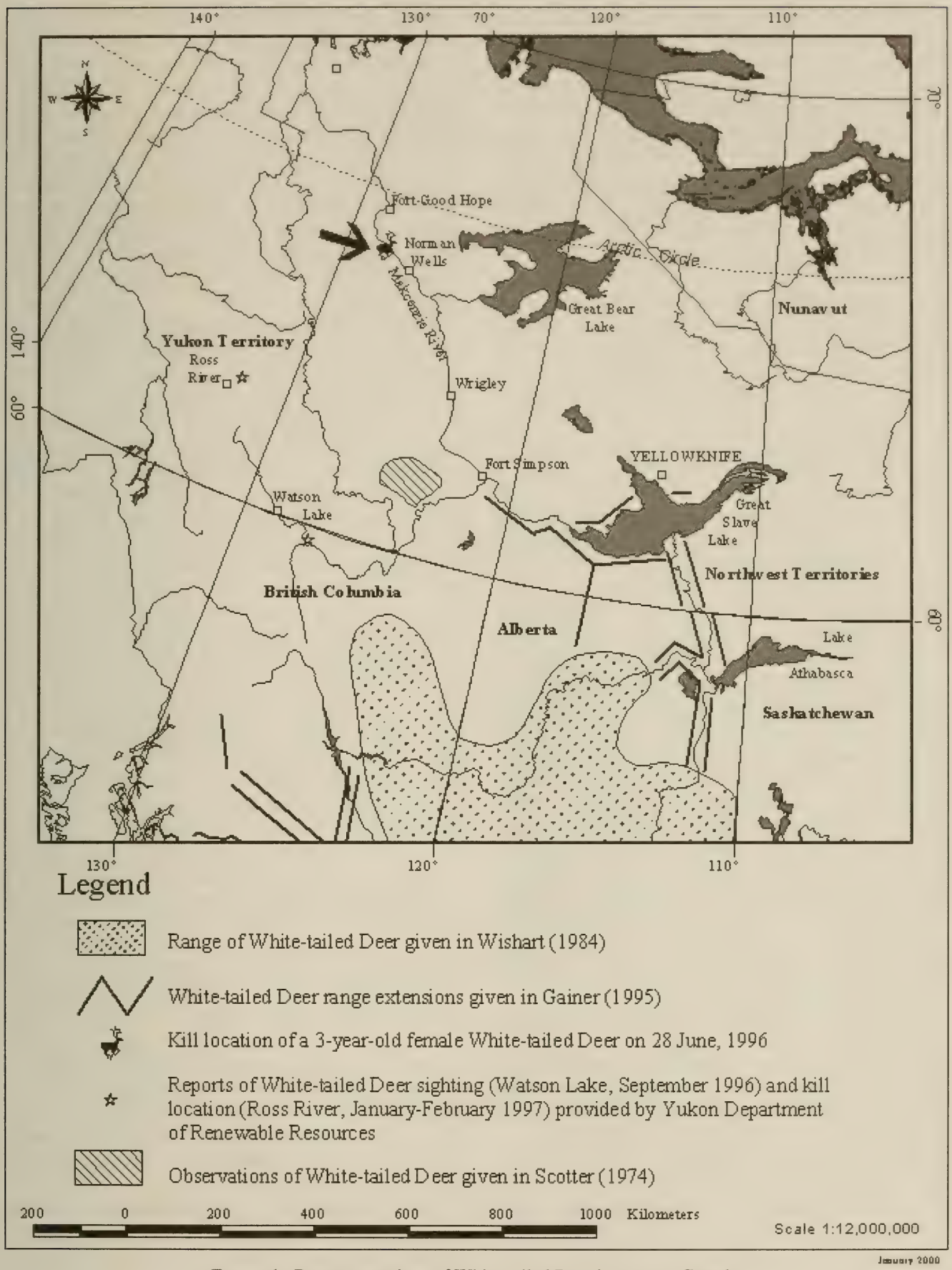

FIGURE 1. Range extensions of White-tailed Deer in western Canada.

On 28 June 1996, Lawrence Jackson, a Sahtu Dene hunter from Fort Good Hope, N.W.T., and three others were travelling upriver by boat on the Mackenzie River from Fort Good Hope to Norman Wells. They encountered a deer swimming across the river from west to east at 65° 37′ N; 128° 16′ W,

approximately 100 km south of the Arctic Circle (Figure 1). Under the *N.W.T. Act* and the *N.W.T. Wildlife Act*, holders of aboriginal general hunting licences have the right to take non-endangered species of Cervidae for food during any season. The four hunters killed the deer and brought the head to the Department of Resources, Wildlife & Economic Development (DRWED) in Norman Wells for species identification. Gainer (1995) also reported that hunters killed White-tailed Deer that were swimming across the Mackenzie River near its outflow from Great Slave Lake at Fort Providence.

Mr. Jackson reported that the deer was in good shape and had good abdominal and back fat deposits. Head measurements (to the nearest 0.5 cm) were: neck circumference — 13.0 cm; zygomatic width — 12.5 cm; straight head length — 11.5 cm; contour head length — 14.0 cm; left ear length — 15.5 cm. There were no antlers or antler pedicels and Mr. Jackson confirmed that it was a female.

Resource Officers from DRWED and the author identified the specimen as a White-tailed Deer and took photographs for documentation (on file with DRWED, Norman Wells, N.W.T.). We extracted a lower incisor for age classification (Matson's, Milltown, Montana) and hair and tissue samples for species identification (Forensic Laboratory, Alberta Natural Resources Service, Edmonton, Alberta). A count of cementum annuli determined the animal was 3 ± 0-years-old (Gary Matson, personal communication; Matson's file #AW120996-280). The tissue sample was analyzed by polyacrylamide gel electrophoresis, electrophoresis for phosphoglucose isomerase (PGI), superoxide dismutase (SOD), and isoelectric focusing erythrocyte acid phosphatase (EAP) with known species standards. The PGI test ruled out Wapiti (*Cervus elaphus*), the SOD test ruled out Caribou (*Rangifer tarandus*), and the EAP ruled out Mule Deer (*Odocoileus hemionus*). The enzyme test results confirmed that the tissue came from a White-tailed Deer (Forensic Laboratory Report # 96-86, Alberta Natural Resources Service, Edmonton, Alberta).

This record of a White-tailed Deer within 100 km of the Arctic Circle is the most northern record in North America. There are no previous records of this species in the Mackenzie River valley west of Great Bear Lake. The nearest records are from 300 km south of Norman Wells. Mr. Albert Moses of the Pehdzeh Ki First Nation in Wrigley reported that two White-tailed Deer were seen 20 km south of Wrigley on the east side of the Mackenzie River (ca. 63° 13′ N; 123° 23′ W) in 1997 (Figure 1). Mr. Moses also reported that a local trapper shot and killed a White-tailed Deer on his trapline several years ago near Wrigley.

On the evening of 23 September 1996, two White-tailed Deer were observed by two Yukon Department of Renewable Resources (DRR) Conservation Officers about 20 km south of the Yukon-British Columbia border (Yukon DRR Occurrence Report no. WH96-199; Figure 1). The Deer were feeding in a ditch along the Alaska Highway and were tentatively identified as an adult female and a yearling. On 5 February 1997 the carcass of a male White-tailed Deer, field aged at 3 or 4-years-old, was found about 2 km northeast of Ross River site (Kevin Johnstone, Yukon DRR, Ross River, Yukon, personal communication). From available evidence at the kill site (ca. 62° 00' N; 132° 00' W), Yukon DRR personnel assume that this Deer had died sometime in late January or early February 1997.

There are no records of White-tailed Deer occurring in Alaska north of the 60th parallel (A. Franzmann, Soldotna, Alaska, and L. Adams, Anchorage, Alaska, personal communications).

These recent and historical sightings of White-tailed Deer in the N.W.T. and Yukon indicate the northern limit of White-tailed Deer is poorly defined. The factors leading to an expansion could be milder weather, increased White-tailed Deer habitat as a result of human settlement, absence of ungulate competition, and scarcity of predators (Wishart 1984). The Mackenzie Basin experienced a warming trend of 1.5°C in the twentieth century and is expected to warm by a further 4 to 5°C by the middle of the twenty-first century (Cohen 1997). However, the N.W.T. still has sparse human settlement (0.02 person/km^2), populations of native ungulates — Wood Bison (*Bison bison*), Moose (*Alces alces*), Woodland Caribou (*Rangifer tarandus caribou*), and Barrenground Caribou (*R. t. groenlandicus*), and a full complement of large predators — Gray Wolves (*Canis lupus*), Black Bears (*Ursus americanus*), and Grizzly Bears (*U. arctos horribilis*).

Gainer (1995) suggests that seismic lines cleared for oil and gas exploration and extraction activities might serve as a conduit for northern excursions by White-tailed Deer. The White-tailed Deer found near Norman Wells may have traveled north along the 10 m-wide underground oil pipeline right-of-way that stretches along the east side of the Mackenzie River from Norman Wells to northern Alberta. The right-of-way is covered with early regeneration browse species such as Willow (*Salix* spp.) and Red-osier Dogwood (*Cornus stolonifera*). Periodic maintenance ensures that the right-of-way is continually covered with early regeneration species attractive to White-tailed Deer.

The northern extension of White-tailed Deer also provides potential for a concurrent extension of the species' parasites, such as the Meningeal Worm (*Parelaphostrongylus tenuis*) and Winter Tick (*Dermacentor albipictus*), that could be transmitted to local Moose or Caribou populations. Over the past three decades, the Meningeal Worm's range has not extended north or west of the Manitoba-Saskatche-

wan border (Bindernagel and Anderson 1972). Therefore, it probably does not currently parasitize White-tailed Deer in the N.W.T. (W. Samuel, University of Alberta, personal communication; Gainer 1995). Similarly, winter ticks currently occur only at low levels in the Yukon (Samuel 1989), do not naturally occur in Alaska (Zarnke et al. 1990), and are not likely to occur north of the 62° in the N.W.T. (Wilkinson 1967; Samuel 1989). In recent years, a few reports of winter ticks on moose in the vicinity of Fort Simpson have been received (J. Antoine, Fort Simpson, N.W.T., personal communication).

Global warming is expected to change the distribution of many wildlife species and their habitats in the N.W.T. over the next century (Cohen 1997). Increased fire activity and changing growing seasons as a result of global warming (Hartley and Marshall 1997) are most likely to enhance the ability of early-succession species, such as White-tailed Deer, to expand their range. Additionally, global warming may lead to increased capacity for agriculture in the N.W.T. (Cohen 1997), which would favour White-tailed Deer and Mule Deer over Moose, Caribou, and Bison.

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Northern Gannet, *Morus bassanus,* Nesting on Whitehorse Island, New Brunswick

SEAN CORRIGAN[1] and ANTONY W. DIAMOND[2]

[1]Biology Department, University of New Brunswick, Bag Service 45111, Fredericton, New Brunswick E3B 6E1, Canada
[2]Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick E3B 6E1, Canada

Corrigan, Sean, and Antony W. Diamond. 2001. Northern Gannet *Morus bassanus* nesting on Whitehorse Island, New Brunswick. Canadian Field-Naturalist. 115(1): 176–177.

In 1999 a pair of Northern Gannets raised a chick for several weeks among a colony of Double-crested Cormorants on Whitehorse Island, New Brunswick. This is the first confirmed breeing of this species in New Brunswick, and in the Bay of Fundy, since 1880. The chick had disappeared by early September (long before it could have fledged), and may have been taken by Bald Eagles. Previous attempts at nesting in the region since the early 1970s are documented.

Key Words: Northern Gannet, *Morus bassanus*, breeding, Bay of Fundy, New Brunswick.

Northern Gannets (hereafter "gannets") have not nested in the Maritime Provinces since about 1880 (Tufts 1986) but have been prospecting potential breeding sites in the outer Bay of Fundy at least since the early 1970s (Huntingdon 1975*; Gaskin and Smith 1979). During the summer of 1999, S.C. frequently passed close to Whitehorse Island (44° 59′ N, 66° 52′W) by boat and observed up to six adult gannets on the top of a cliff in a large colony of nesting Double-crested Cormorants *Phalacrocorax auritus*. A photograph he took on 11 June shows three adult gannets on three separate nests. On 22 July both authors landed on the island, accompanied by K. Mawhinney and P. Edwards, in order to verify the breeding status of the gannets. As we approached the cliff-top from the north, one adult flew off, but one remained on a nest and allowed approach to within 5 metres. At that point the bird stood up on the nest and revealed a single chick, naked but showing down feathers beginning to appear on the back; from the early stage of feathering the chick was no more than one week old (Nelson 1978, page 90). There was no sign of any other gannet nests nearby.

On 22 August, S.C. landed on Whitehorse to observe the nest. As he approached (approximately 20 metres away) a single adult flew off leaving the chick unattended. At that time tail feathers were starting to appear, suggesting the chick was at least 5 weeks old (Nelson 1978). By the time S.C. returned to the boat, two adult gannets had returned to the nest. On 23 August, three adult gannets and one chick were observed at the same place from a boat.

On 13 September, S.C. returned to Whitehorse to observe the chick. No birds were visible from below the cliff. About 12 cormorants and 3 immature Bald Eagles *Haliaeetus leucocephalus* were on the cliffs; the top of the island was completely vacant. The nest was empty, and several pieces of white down were found on nearby vegetation.

Discussion

Gannets evidently nested in the southwest Bay of Fundy when Europeans first explored the area; the account by Denys (1672), from his visits in the 1640s, echoed Champlain's reference to gannets nesting on the Wolves Archipelago (a group of islands 12 km south-east of Whitehorse). The last breeding record is from Gannet Rock, New Brunswick (44° 30′N, 66° 47′ W) between 1830 (when the lighthouse was built) and 1865 (Nelson 1978). However gannets bred on the Nova Scotia side of the Bay of Fundy until about1880, when they were extirpated (by over-exploitation by fishermen) from the Gannet Rock in Nova Scotia, south of the Tusket Islands (Tufts 1986).

Gannets have been observed in the Grand Manan area in circumstances suggesting attempts to breed since the early 1970s. Huntingdon (1975*) described a single gannet 'defending a territory' at the south end of Kent Island (44° 34′N, 66° 45′W) in 1972; two were present the next year, and in May 1974 two were observed courting, gathering nest material and building a nest, but had disappeared by mid June. On Whitehorse itself, "in 1977, 1978, and 1979, a pair of gannets has been nesting" (Gaskin and Smith 1979); no further details were given, and there are contradictory data in Canadian Wildlife Service (1979) and Lock (1982*) from a ground-count on Whitehorse on 31 May 1979 which found no gannets. Lock (1982*, page 25) specifically noted the absence of "gannets, which had been reported roosting in this colony". In view of these inconsistencies in the 1979 observations, we view our record of nesting on Whitehorse Island in 1999 as the first fully documented record of Northern Gannets breeding in the Bay of Fundy since the 1880s.

*See Documents Cited section.

Acknowledgments

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Unusual Harlequin Duck, *Histrionicus histrionicus*, Nest Site Discovered in Central Labrador

TONY E. CHUBBS[1], BRUCE MACTAVISH[2], KEITH ORAM[3,4], PERRY G. TRIMPER[3], KATHY KNOX[2] and R. IAN GOUDIE[5]

[1]Department of National Defence, 5 Wing Goose Bay, Box 7002, Postal Station A, Happy Valley – Goose Bay, Labrador, Newfoundland A0P 1S0, Canada
[2]Jacques Whitford Environment, 607 Torbay Road, St. John's, Newfoundland A1A 4Y6, Canada
[3]Jacques Whitford Environment Limited, Box 274, Postal Station C, Happy Valley – Goose Bay, Labrador, Newfoundland A0P 1C0, Canada
[4]Present address: Box 782, Postal Station C, Happy Valley — Goose Bay, Labrador, Newfoundland A0P 1C0, Canada
[5]Memorial University of Newfoundland, Department of Biology, St. John's, Newfoundland A1B 3X9, Canada

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During telemetry monitoring of adult Harlequin Ducks, *Histrionicus histrionicus*, in 1999, a female was radio-tracked to her nest site. The nest site, only the third recorded in Labrador, was unusual, as it was located 108 m from the nearest river, in open spruce-lichen boreal forest.

Key Words: Harlequin Duck, *Histrionicus histrionicus*, nest, habitat, Labrador.

In May 1999, we began telemetry monitoring of Harlequin Ducks (*Histrionicus histrionicus*) in central Labrador to investigate movement patterns of adult pairs in spring. The objective was to determine if spring aerial surveys provided adequate information on which to base measures to protect occupied breeding habitat from potential disturbance by low flying military aircraft, a commitment to protection identified by the Department of National Defence (DND 1994*). Little information is known on the breeding habitat of the eastern North American population which was designated as endangered in 1990 (COSEWIC 1998*).

On 26 May 1999, we captured an adult female Harlequin Duck near Fig River (53°04'N, 63°08'W), a tributary of the Churchill River in central Labrador. The river section around the capture site ranged in width from 50 to 150 m and consisted of a series of five pools interspersed with rapids and two small islands. We marked the female with a standard metal band, an alpha numeric, colored (1J, yellow) plastic leg band and attached a tail-mounted VHF transmitter (148.441 MHz). The transmitter signal

*See Documents Cited section.

was heard on the river < 50 m from the capture site on 28 May but the bird was not observed. Telemetry locations on 29 May, 5 and 11 June, were approximately 700 m downstream of the capture site, adjacent to the nest location. Since the bird was not observed on the river during these three surveys, we assumed that she was nesting. She was located using radio-telemetry on 12 June 1999, and flushed when approached. A search of the area revealed a nest on the ground. This is the first Harlequin Duck nest discovered in central Labrador, whereas two others have been previously described on coastal rivers in northern Labrador (Rodway et. al 1998; Chubbs et. al 2000).

The nest was located 108 m from the nearest edge of the river and 250 m from where the female was captured. Generally, Harlequin Ducks do not nest far (< 5 m) from water (Robertson and Goudie 1999). The 22 cm diameter nest was concealed beneath the layered branches at the base of a 10 m tall Black Spruce (*Picea mariana*) tree. Surrounding vegetation consisted of open spruce-lichen forest, a habitat quite dissimilar to others described both in Labrador (Rodway et al. 1998; Chubbs et al. 2000) and elsewhere in North America (Robertson and Goudie 1999). Black Spruce branches that grew into the ground formed a tent-like enclosure which provided 100% vertical nest cover; similar to many nest sites described for the western Harlequin Duck population (Bruner 1997; Robertson and Goudie 1999). The nest bowl was lined with down and dead Black Spruce twigs and contained five eggs. The opening to the nest site was 33 cm high and 15 cm wide. Ground cover within 5 m of the net was 95% caribou lichen (*Cladina* sp.) and 5% Sheep Laurel (*Kalmia angustifolia*). The forest was 100% mature Black Spruce, with trees spaced approximately 5 m apart. The nest site was found abandoned when revisited on 19 June 1999. The clutch was missing and assumed depredated. The fate of the female is unknown as she was not relocated or observed after 12 June 1999 and surveys were discontinued after 19 June 1999. However, she was resighted in 2000.

Information on Harlequin Duck nesting habitat in Labrador is limited to two other nest sites, both on coastal rivers (Rodway et al. 1998; Chubbs et al. 2000). Our nest site was in a forested rather than a riparian habitat, and was relatively far from water. Although, the nesting site was dissimilar to that described by Rodway et al. (1998) and Chubbs et al. (2000), all nests found in Labrador have been near rivers with small islands and channels and relatively calm steadies. Other nesting records in North America indicate that Harlequin Ducks select a variety of nesting sites including rock crevices, cliff ledges, woody debris, tree cavities, and islands (Brodeur et al. 1998; Rodway et al. 1998; Bruner 1997). It appears that the selection of favorable breeding locations by Harlequin Ducks in Labrador may be more dependent on the type and characteristics of the river rather than the microhabitat in the vicinity of the nest site.

Based upon our telemetry locations and that five eggs had been laid by 12 June, we suspect that the female had initiated nesting at least as early as 29 May, resulting in our failure to locate her on the river. In addition, based on the relative proximity of other nest sites to water described in Labrador and elsewhere, our search strategy focussed on the shoreline.

We speculate that the nest may have been so distant from the shore due to extraordinary high spring water levels in this region, which may take two to three weeks to recede. Additionally, numerous observations of Mink (*Mustela vison*) along rivers in this region suggest that female Harlequin Ducks may be nesting far from rivers to avoid these predators.

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"Standing Over" And "Hugging" in Wild Wolves, *Canis lupus*

L. DAVID MECH[1]

Biological Resources Division, U.S. Geological Survey, Northern Prairie, Wildlife Research Center, 8711 - 37th St., SE, Jamestown, North Dakota, 58401-7317, USA
[1]Mailing address: North Central Research Station, 1992 Folwell Avenue, St. Paul, Minnesota 55108, USA

Mech, L. David. 2001. "Standing over" and "hugging" in wild Wolves, *Canis lupus*. The Canadian Field-Naturalist 115(1): 179–181.

During six summers, I observed "standing over" (SO) and "hugging" in a pack of wild Wolves (*Canis lupus*) habituated to me. In SO, one Wolf positions its groin above a recumbent Wolf's nose. I observed SO among all yearling and older Wolves for 1–180 seconds ($\bar{x}$ = 69 ± 46 S.D.; N = 16). SO appeared to be primarily female-oriented and may inform each Wolf of the reproductive status of the other. I observed "hugging" five times and only during years when food competition was minimal.

Key Words: Wolf, *Canis lupus*, behavior, standing over, affection, reproduction.

To help understand the nature of relationships among members of Wolf (*Canis lupus*) packs, the postures of interacting animals are important clues (Schenkel 1947; Zimen 1982; Goodman and Klinghammer 1985). However, because of the elusiveness of Wolves, it is difficult to observe their behavior under natural conditions (Mech 1974). Even the few observational studies that have been conducted of wild Wolves (Murie 1944; Clark 1971; Carbyn 1974; Haber 1977) have failed to quantify most Wolf postural behaviors, including "standing over" (Schenkel 1947) and "hugging" (Goodman and Klinghammer 1985). I attempt here to quantify and analyze these two behaviors in one wild Wolf pack.

Methods

Study Area

This study was conducted during six summers from 1988 through 1996 on Ellesmere Island, Northwest Territories, Canada (80° N, 86° W). There, Wolves prey on Arctic Hares (*Lepus arcticus*), Muskoxen (*Ovibos moschatus*), and Peary Caribou (*Rangifer tarandus pearyi*), and live far enough from exploitation and persecution by humans that they are relatively unafraid of people (Mech 1988, 1995). During 1986, I habituated a pack of Wolves there to my presence and reinforced the habituation annually.

The pack frequented the same area each summer and usually used the same den or nearby dens, but pack composition varied annually (Mech 1995). The habituation allowed an assistant and me to remain with the Wolves daily, to recognize them individually, and to watch them regularly from as close as 1 m (Mech 1988, 1995; National Geographic 1988). During 1759 h of observation, we noted each time an individual Wolf interacted with another Wolf, except for pups, which were not distinguishable from each other.

"Standing over" (SO) is a low-intensity display in which one Wolf casually approaches a recumbent Wolf and stands over or along side the recumbent Wolf so that the standing Wolf's groin is positioned above the recumbent Wolf's nose. I found no set pattern of behavior before or after SO by either the active Wolf or the recumbent Wolf — SO took place in a variety of contexts.

In "hugging," which I have never seen described in wild Wolves and only once in captives (Goodman and Klinghammer 1985), an individual Wolf puts its front legs around the head and neck of another while each lies on its side chest-to-chest, or on its haunches facing each other, or side-by-side on haunches with one placing front legs around the other's neck.

Only a few instances of SO were observed each year. Therefore sample sizes were too small for statistical comparisons by sex and age class within years. Pooling across years for statistical comparisons was inappropriate because opportunities for

*See Documents Cited section.

TABLE 1. Distribution of 35 observations of "Standing Over" amongst various dyads of Ellesmere Island Wolves during summer. (BM = breeding male; BF = breeding female; YF = young[1] female; YM = young[1] male; PF = post-reproductive female.)

Year	BM BF	BM YF	BM YM	BF BM	BF YF	BF YM	YM BF	YM YF	YM BM	YF BM	YF BF	YF YM	BF PF	PF BF	PF BM	BM PF
1988	0	0	1	0	1	0	0	0	0	1	1	0	-	-	-	-
1990	0	-	-	2	-	-	-	-	-	-	-	-	9	2	1	0
1991	0	-	-	2	-	-	-	-	-	-	-	-	2	2	1	1
1992	0	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
1994[1]	0	0	0	1	2	1	0	0	1	1	0	0	-	-	-	-
1996	0	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Observed	0.00	0.00	1.00	8.00	3.00	1.00	0.00	0.00	1.00	2.00	1.00	0.00	11.00	4.00	2.00	1.00
Expected[2]	5.25	1.75	1.75	5.25	1.75	1.75	1.75	1.75	1.75	1.75	1.75	1.75	1.75	1.75	1.75	1.75

[1]In 1988, the YF and YM roles were yearlings; in 1994, 2-year olds.
[2]Expected if interactions were proportional to opportunities based on years present.

participation by Wolves of various sex and classes varied among years.

Results

During eight summers from 1988–1998 (excluding 1989 and 1995) I observed SO 35 times during six of those summers (Table 1). During the same period, I saw dominance interactions 217 times (Mech 1999). SO took place among all yearling and older Wolves in both the standing and recumbent positions for 1–180 seconds ($\bar{x}$ = 69 ± 46 S.D.; N = 16), although not in all possible combinations (Table 1). In 14% of the observations, the lying Wolf sniffed at the groin or genitals of the standing Wolf.

The most intensive SO I ever observed was at 1647 hours on 2 July 1990, when the new breeding female (three-year-old "Whitey") stood over her post-reproductive mother ("Mom") for 3 minutes: My field notes taken at the time state: "When Mom moved her nose to one side or the other of Whitey's groin, Whitey would move her groin over Mom's nose. Mom appeared nonchalant and disinterested, although she did sniff both the inside and outside of Whitey's legs casually. Whitey remained intent and stiff-legged and persistent throughout the display."

Standing over appeared to be primarily female-oriented, with the post-reproductive female involved most often. The active Wolf was most often the breeding female. The post-reproductive female was the active Wolf next most often and was the recumbent Wolf most often. It also seems important that during the first year (1990) that a three-year-old daughter replaced her mother as breeder (Mech 1995), the daughter stood over the mother the most often of all possible dyads in all years (Table 1). I observed hugging five times, four of which were in 1990 (Table 2). All possible dyads of the breeding male, breeding female and post-reproductive female engaged in hugging.

Discussion

Behaviorists disagree on the meaning or significance of SO. Schenkel (1947, translation by F. H. Harrington) saw SO in his captive Wolves only during "peaceful" times and did not seem to regard it as a dominance-related posture. He believed that SO " . . . is probably derived from the presentation of the genitalia by the young, behaviour that is released (stimulated) by the licking by the mother." However, I never saw any genital licking associated with SO. Zimen (1982) listed SO as one of 48 postures he observed but stated nothing more about it except that it was a "neutral" posture. Goodman and Klinghammer (1985) listed SO in the following categories of behavior: aggressive-elicited; aggressive-food related; aggressive-sex related; care-giving, care-solicitation; greeting; and

TABLE 2. Description of "hugging" in members of the Ellesmere Island Wolf pack.

Date	Description
30 June 1990	Breeding male and post-reproductive female lie on side chest-to-chest, and each puts front legs over the other
14 July 1990	Post-reproductive female hugs breeding daughter from behind 3 times, sitting, chest to back but rumps were side-by-side
14 July 1990	Breeding female and breeding male lie down facing each other and put legs over each other's shoulders and nuzzle each other
17 July 1990	Breeding female and breeding male face each other lying down and female puts legs around male's neck
9 July 1992	Breeding female lies with breeding male and places both legs around his neck, but he jumps up

play-agonistic. I did not see any hostility or aggressiveness associated with SO, but my observations were made only in summer, the nadir of Wolf breeding physiology (Seal et al. 1979). R. O. Peterson (personal communication), during 28 winters observing Isle Royale Wolves, saw seven cases of SO, four of which were between breeders; he concluded that "SO came out as a pretty minor behavior, and depending on context appeared to have significance in dominance expression and courtship." Derix et al. (1994) grouped SO with behaviors they considered sexual in their captive pack.

Three clues from my data (Table 1) about the significance of SO are (1) that any pack member could be an active or passive participant, (2) the breeding female, post-reproductive female, and breeding male were most involved, and (3) in at least some of the cases, genital or inguinal sniffing was involved. From these data, I propose that SO is a posture that simply informs each Wolf of the reproductive status of the other, i.e., gender and degree of reproductive maturity and readiness.

Goodman and Klinghammer (1985) interpreted hugging as an agonistic, greeting, or courtship display. However, in the context in which I observed the behavior during summer, it appeared more to be a deliberate display of friendliness and affection than to fit in any of the other categories. I cannot explain why I only observed hugging in 1990, and an aborted attempt in 1992 (Table 2), except that in 1990 there were three adult Wolves and only a single pup in the pack. Thus food competition was minimal.

These observations greatly extend information about Wolf behavior, previously only described in captive situations, by placing the behaviors in their natural context. The hypotheses offered about their interpretation can be used to explore further their significance.

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Limb Mutilations in Snapping Turtles, *Chelydra serpentina*

RAYMOND A. SAUMURE[1,2]

[1]Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Road, Ste-Anne-de-Bellevue, Québec H9X 3V9, Canada
[2]Present address: Shark Reef at Mandalay Bay, 3950 Las Vegas Boulevard South, Las Vegas, Nevada 89119, USA

Saumure, Raymond A. 2001. Limb mutilations in Snapping Turtles, *Chelydra serpentina*. Canadian Field-Naturalist 115(1): 182–184.

Adult Snapping Turtles (*Chelydra serpentina*) with mutilated limbs were captured in Ontario and Québec. Although similar injuries have been reported for several other species of North American turtles, this is the first documented report of such mutilations in this species. The implications of such injuries are discussed.

Key Words: Snapping Turtle, *Chelydra serpentina*, mutilations, leech, *Placobdella parasitica*, Ontario, Québec.

Limb mutilations have been reported for several species of North American turtles. Nemuras (1966) noted that Spotted Turtles (*Clemmys guttata*) often had limbs missing, but did not report exact figures. A later study on *C. guttata* reported that 5.8% of a population (n = 207) in Pennsylvania had missing limbs (Ernst 1976). A Musk Turtle (*Sternotherus odoratus*) population (n = 204) at the same Pennsylvania location exhibited a limb loss rate of 4.9% (Ernst 1986). Belinky and Belinky (1974) reported having encountered many Wood Turtles (*Clemmys insculpta*) with mutilated limbs. Harding (1985), however, was the first to quantify limb loss in this semi-terrestrial species. He found that 12.5% of Wood Turtles in a northern Michigan forest population (n = 337) had mutilated limbs. In most cases of limb mutilations in *C. insculpta*, the Raccoon (*Procyon lotor*) was observed and/or suspected. Subsequently, there have been numerous reports of limb loss in Wood Turtles. Foscarini (1994) reported a limb mutilation rate of 12.9% from an agricultural population (n = 270) in Ontario. Tuttle (1996) documented a rate of 9% from an agricultural population (n = 82) in New Hampshire. Saumure and Bider (1998) found rates of 15.2% and 32.3% for Québec agricultural (n = 33) and forest (n = 31) population samples, respectively. Waller and Micucci (1997) reported that fewer than 13% of *Geochelone chilensis* (n = 59) in Argentina had missing limbs. The lowest percentage of mutilated turtles was reported by Meek (1989) for *Testudo hermanni* in Yugoslavia, where only two of 213 turtles (0.94%) had missing limbs. To date, there have been no published reports of limb loss in Snapping Turtles, *Chelydra serpentina*. Herein, I report two instances of limb mutilations in *C. serpentina* and discuss the implications of such injuries.

On 23 June 1994, I encountered an adult female *Chelydra serpentina* nesting in a gravel pit located along an old logging road, approximately 30 m from a stream in a mixed-deciduous forest in Pontiac County, Québec (45°53′N; 76°12′W). This specimen had both anterior limbs amputated through the radius and ulna bones, at a point close to their junction with the humerus. The wounds were completely healed. On 13 June 1996, this turtle was recaptured in the same gravel pit, measured, and photographed (Figure 1). This specimen had a carapace length of 289.4 mm. Of note is the fact that this turtle produced clutches in at least two of three nesting seasons, despite being devoid of anterior limbs. This suggests that the foraging ability of this turtle was not seriously compromised by the mutilations.

On 19 August 1995, an adult male *Chelydra serpentina* was captured as it crossed a road near Port Royal, Big Creek National Wildlife Area (BCNWA), Regional Municipality of Haldimand-Norfolk, Ontario (42°35′N; 80°31′W). The turtle had a carapace length of 248.2 mm. This particular turtle was noticed because it appeared to be limping, and because Snapping Turtles are frequently run over ($\bar{x}$ = 68/year) by motorized vehicles in this area (Ashley and Robinson 1996). The specimen was missing its right posterior limb, which had been severed sufficiently high on the femur so as to leave the turtle without a stump to walk on (Figure 2). The point of amputation was completely healed, although the skin to the right of the posterior lobe of the plastron was chafed and bleeding. This chafing appears to have been the result of friction between this part of its body and the paved road. The turtle possessed three shallow bloodless gashes of unknown origin on the anterior plastron, only one of which had completely healed shut. Of 229 Snapping Turtles captured between 1992 and 1996 in the BCNWA, only this turtle (0.44 %) had a missing limb. Three adult Smooth Turtle Leeches (*Placobdella parasitica*) were attached to this turtle in the damaged limb socket. This is similar to a report by Saumure and Bider (1996) of leeches parasitizing the injured areas of mutilated Wood Turtles (*Clemmys insculpta*). Hendricks et al. (1971) hypothesized that leeches could readily colonize sick or injured turtles because of the host's inability to avoid or rid themselves of the parasites.

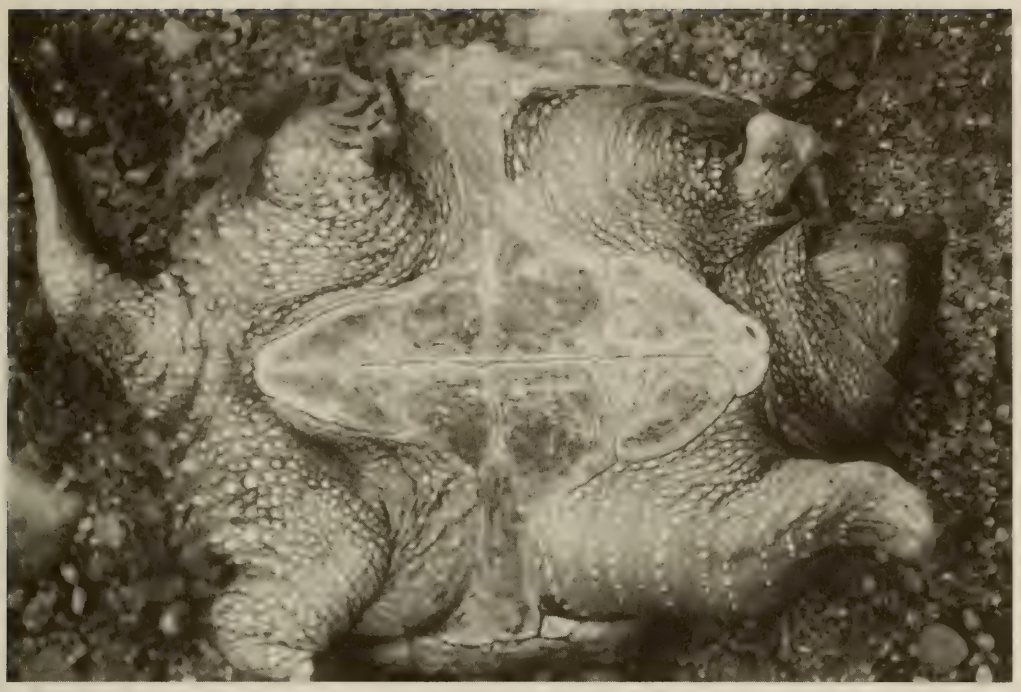

FIGURE 1. *Chelydra serpentina* from Pontiac County, Québec, with mutilated anterior forelimbs.

The absence of previous reports of limb mutilation in Snapping Turtles is not surprising, as the species has a number of physical and behavioural characteristics which serve to dissuade potential predators. Wild adult male *Chelydra* can reach a maximum carapace length of 494 mm and weigh as much as 34 kg (Conant and Collins 1991: 41). When harassed, they can also exude a foul smelling musk from glands located on the shell bridge (Carr 1952: 65). Moreover, a Snapping Turtle will tilt and lower the portion of its shell under attack, while turning to face its aggressor (Dodd and Brodie 1975). Lastly, the Snapping Turtle has a distinctly belligerent nature which it backs up by lightning quick strikes at speeds exceeding 78 ms (Lauder and Prendergast 1992). Therefore, it is not surprising that encounters between Raccoons and nesting female Snapping Turtles do not lead to predation attempts on the turtles (Congdon et al. 1987).

Known causes of limb loss in turtles include attacks by mammalian predators (e.g., Harding 1985) and agricultural mowers (Ernst 1976; Tuttle 1996). It is, however, improbable that an adult Raccoon could gnaw off both anterior limbs of a fully alert adult Snapping Turtle. Consequently, it is much more likely that the attack occurred when the turtle was small and relatively defenseless (e.g., Robinson 1989; Walley 1993), or while it was in a state of torpor during hibernation (e.g., Brooks et al. 1991). Due to the remote location of the Pontiac site, it is unlikely that an agricultural mower was the cause of the amputations. However, limb loss due to agricultural mowers or predation cannot be ruled out for the BCNWA turtle. Brooks (personal communication) reports that the observed frequency of limb loss in *Chelydra serpentina* at his Algonquin Park, Hamilton Harbour, and Lake Erie research sites in Ontario was also $< 1\%$, despite the various types of predators and anthropogenic disturbances at these sites.

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FIGURE 2. *Chelydra serpentina* from Regional Municipality of Haldimand-Norfolk, Ontario, with amputated right posterior limb and two leeches (*Placobdella parasitica*) attached posterior to the injury.

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News and Comment

Notices

American Birding Association Ludlow Griscom Award for Publications in Field Ornithology: W. Earl Godfrey, June 2000

On 29 June 2000, the Board of Directors of the American Birding Association presented the ABA Ludlow Griscom Award "recognizing professional excellence and achievements in field ornithology literature" to W. Earl Godfrey. The award included a framed Certificate of Appreciation, recognizing his book *The Birds of Canada* 1966, revised 1986 and a plaque. An additional plaque and a pair of state-of-the-art binoculars were presented by co-sponsor Bushnell Sports Optics. Dr. Godfrey has more than 200 publications, the result of field investigations and museum analysis of bird populations including a series of monographs on regional avifaunas of Canada produced by the (then) National Museum of Canada and others in *The Canadian Field-Naturalist*. He was curator of Ornithology at the National Museum from 1947, and later Chief of the Vertebrate Zoology Division, until he retired from these positions at the end of 1976, but has continued as a Curator Emeritus and Research Associate of the (now) Canadian Musuem of Nature to the present. He has long been an Associate Editor for *The Candian Field-Naturalist* and is an Honorary Member of the Ottawa Field-Naturalists' Club.

Froglog: Newsletter of the Declining Amphibian Populations Task Force (42)

The December 2000 issue contains: A short note about the status and abundance of caecilian populations [Daniel Hofer] — A Malformed *Dendrobates tinctorius* from French Guiana [David Massemin and Christian Marty] — Amphibian declines in Ecuador: overview and first report of chytridiomycosis from South America [Santiago R. Ron and Andres Merino] (also in Spanish) — Scientific meeting raises awareness of amphibian declines in Asia [Vanc Vredenburg, Yuezhao Wang, and Gary Fellers — Froglog Shorts — Publications of Interest.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of The World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by The Open University, The World Congress of Herpetology, The Smithsonian Institution, and Harvard University. The newsletter is Edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail: daptf@open.ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P. O. Box 39, Michigan 48068-0039, USA. *Froglog* can be accessed at http://www2.open.ac.uk/biology/froglog/

Marine Turtle Newsletter (91)

The January 2001 issue, 24 pages, contains: GUEST EDITORIAL: Developing sea turtle ecotourism in French Guiana: Perils and practicalities — ARTICLES: Growth rates of juvinile Green Turtles (*Chelonia mydas*) from Atlantic coastal waters of S. Lucie County, Florida, USA — Helping people help the turtles: The work of Projeto *TAMAR-IBAMA* in Almofala, Brazil — NOTES: A new kind of illegal trade of Marine Turtles in Uraguay — MEETING REPORTS — ANNOUNCEMENTS — BOOK REVIEWS — NEWS & LEGAL BRIEFS, — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Wales, Swansea, Singleton Park, Swansea SA2 8PP Wales, United Kingdom; e-mail MTN@swan.ac.uk; Fax +44 1792 295447. Subscriptions to the MTN and donations towards the production of MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be sent to Marine Turtle Newsletter c/o Chelonian Research Foundation, 168 Goodrich Street, Lunenburg, Massachusetts 01462 USA; e-mail RhodinCRF@aol.com; fax + 1 978 582 6279. MTN website is: <http://www.seaturtle.org/mtn/>

Canadian Species at Risk November 2000

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has issued *Canadian Species at Risk November 2000*, 24 pages. The list gives (1) all species designated and all status re-assessments, in five Risk categories (Extinct, Extirpated, Endangered, Threatened and Special Concern), (2) Not at Risk and (3) Data Deficient.

It is available from COSEWIC Secretariat, Chief Coleen Hyslop, c/o Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3. See Web site: http://www.cosewic.gc.ca

The Boreal Dip Net 5(1)

The December 2000 issue of the Newsletter of the Canadian Amphibian and Conservation Network/ Reseau Canadien de Conservation des Amphibiens and Reptiles reports: CARCN/RCCAR 1999-2000 initiatives — Board of Directors Meetings — Thank You to Sponsors — Forest Stewartship Recognition Award — Field trip — Extended Abstracts from keynote speakes: James P. Gibbs, Betsie B. Rothermel and Raymond D. Semlitsch — Forest Harvesting and Amphibians — List of papers presented at CARCN/RCCAR Meeting [September 2000, Penticton, British Columbia] — Digital Frog International & CARCN/RCCAR Scholarship Winner — US DOI Amphibian Declines Program — Turtle nests created in Laurel Creek Conservation Area.

For membership and other information on the CARCN/RCCAR contact Bruce Pauli, Canadian Wildlife Service, National Wildlife Reseach Centre, 100 Gamelin Boulevard, Hull, Quebec, Canada K1A OH3.

Sea Wind: Bulletin of Ocean Voice International 14(4)

The October-December 2000 issue, 40 pages, contains: Conserving Tanzanian Coral Reefs and Mangroves: A support request — Beauty if the reefs — Kapis Shells: A diminishing part of Filipino heritage — Novel on commercial fishing: A request — Water a fundamental right, say Bolivian poor — World Fora of Fishers — Conference: Putting fisher's knowledge to work — Then and Now — Quotes — Members Feedback — Sea News — Booke Nooke — Kids Korner — Please help us! Tiny cards to save big oceans.

Sea Wind is a publication of Ocean Voice International and is edited by Donald E. McAllister (e-mail: mcall@superaje.com) and is available though subscription or membership from Voice International Inc., 2255 Carling Avenue, Suite 400, Ottawa, Ontario K2B 1A6, Canada; phone (613) 721-4541; fax (613) 721- 4562; Angela Jellett, Executive Director at: e-mail: <ovi@cyberus.ca>; home page: <http://www.ovi.ca>

Recovery (17)

The October 2000 issue contains: Landowners join recovery effort (Robert Wenting) — Working group addresses recovery issues — Migratory scientist retires [Charles (Chuck) Dauphine] — Conserving nature at regional and continental scales: a scientific program for North America (Michael E. Soule and John Terborgh — Communities conserve "habitat connections" (Jean Langlois) — COSEWIC Update: Aboriginal knowledge to improve process (Sara Goulet) — CITES Update: Criteria under review: Experts to consider recommendations this winter (Bertrand Von Arx) — Tracking the world's largest reptile [Leatherback Turtle] (Kathleen Martin).

Recovery is a free newsletter providing information on Canadian species at risk, Coordinated by the Canadian Wildlife Service, and edited and designed by West Hawk Associates, Inc. It is available in either english or french from Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, K1A 0H3 and is accessible at www.cws-scf.ec.gc.ca/es/recovery/archive.html

Ontario Natural Heritage Information Centre Newsletter 6(1)

The Winter 2000 issue contains: SCIENCE: The Big Picture Project: Developing a Natural Heritage Vision for Carolinian Canada — Community Ecology: Rare commentities of Ontario: Coastal marine beach ridges — Zoology: King Rail and Prothonotary Wabler added to Endangered Species Act; Eastern Sand Darter survey; Ontario Odonate surveys — Botany: National Status assessment of Canadian wild orchid speies; 2000 Botanical highlights; Double-crested Cormorant impacts on rare plants; Botanical investigations on Lake Superior — Herpetology: Using the OHS database to identify sites for conservation; Herpetofaunal distribution maps posted on NHIC web — NEWS AND NOTES: NHIC involved in MNR Northern Boreal Initiative; Biological inventory of Kawartha Higlands OLL site; NHIC biologists conduct life science inventory in Polar Bear Prov. Park; Trent University — NHIC internships in conservation biology; NHIC is part of NMR's species at risk program; NHIC Biologists author COSEWIC status reports; NHIC web site renovation; Point Pelee natural history news; NHIC fieldwork in northwestern Ontario; The Association for Biodiversity Information launches NatureServe; Updates to the COSEWIC national species at risk list; NHIC completes hot-spot mapping for NCC — BOOK REVIEWS — NHIC INFORMATION PRODUCTS — NHIC STAFF LIST.

The Ontario Natural Heritage Information Centre Web Page is: http://www.mnr.gov.on.ca/MNR/nhic/nhic.html
Mailing address: 300 Water Street, 2nd Floor, North Tower, P.O. Box 7000, Peterborough, Ontario K9J 8M5, Canada.

Book Reviews

ZOOLOGY

The Birds of British Columbia Volume 3

By R. Wayne Campbell, Neil K. Dawe, Ian MacTaggart-Cowan, John M. Cooper, Gary W. Kaiser, Michael C. E. McNall and G. E. John Smith. 1997. UBC Press, Vancouver. 693 pp., illus $50.00.

The first two volumes of this series, published in 1990, provided a long overdue update on the non-passerine avifauna of British Columbia, as well as a brief history of the ornithology of the province and a detailed overview of its biogeography. Although the authors' reputations led to high expectations for those volumes, they managed to exceed those expectations considerably (see review in Canadian Field-Naturalist 107: 547–548, 1993). Their third volume, covering tyrant flycatchers through vireos, is an even more thorough and splendid achivement, providing both an indispensible collection of scientific data and an easily-read overview of the British Columbia status and distribution of each species in 18 passerine families.

In keeping with the authors' policy of maximizing input, the text of volume 3 begins with a four-page section of acknowledgements to contributors to all aspects of production from collecting and contributing data to writing, reviewing, and/or illustrating portions of the book to financing its production. This is followed by an introductory section on the book's development, general aspects of the birds covered in this volume, and recent developments in avian taxonomy, followed by a checklist of the 91 species of birds covered in the book. The bulk of the text consists of two to 12-page [usually four to eight-page] accounts of species of "regular" occurrence in the province. Thirteen additional one-half to one page accounts of "casual, accidental, extirpated, and extinct species" close the main text. Six appendices (on migration chronology, 1957-1993 Christmas Bird Count data, 1969-1994 Breeding Bird Survey data, a list of 6,498 (!) contributors of observations and two on computer data base details), a list of references cited, an index to species, and short biographies of the authors conclude the tome.

The species accounts are more thorough than those of most "Birds of" works of recent years. The text of each species of regular occurrence includes sections on its overall range, its status in British Columbia, changes in status, nonbreeding and breeding distribution and habitat, nesting data (including nest-sites, nest structure, egg-laying dates, clutch size, brood dates, incubation periods, Brown-headed Cowbird parasitism, etc.), and "remarks" (various aspects of taxonomy, song, conservation status, habitat, and/or behaviour not covered in other sections). Information is included on different areas of the province, and data gaps are identified. The main text for each species is followed by a section on "noteworthy records," arranged by season and geographical portion of the province. Maps, graphs, and black-and-white and/or colour photographs illustrate each bird, its habitat, chronology of occurrence in different parts of the province, locations of nonbreeding and breeding records, and/or nests and eggs. The text of the 13 species of less regular occurrence concentrates on usual range, records of occurrence in British Columbia, references to identification, and sometimes notes on erroneous and/or additional unsubstantiated records in the province.

This book follows the taxonomy and nomenclature recognized by the American Ornithologists' Union to 1995, except that Pacific-slope and Cordilleran flycatchers are treated together as "Western Flycatcher complex." Although the authors agree that those found along the coast are Pacific-slope Flycatchers, they feel that the identity of those in the interior is less certain, and exclude Cordilleran from their check-list. However, Campbell has included it in a subsequent provincial bird list (Wild Bird trust of British Columbia Wildlife Report Number 2, 1998).

As attractive as the first two volumes were, this third volume reaches "coffee table" book quality in many of its photographs. The book also exceeds the previous volumes in the comprehensiveness of the information presented for each species. Information on the British Columbia distribution, status, and population trends of the species covered is complete to December 1995 (with some significant subsequent records added in footnotes and addenda) and whatever was known by then of life history details in British Columbia is summarized, with numerous literature sources cited for follow-up. When details were not available from British Columbia, these are filled in from studies conducted elsewhere. In spite of the book's length and comprehensiveness, it is relatively error-free, with most errors confined to minor grammatical matters, lapses in spelling of people's names or in figure numbers, and failure to differentiate between same-year publications by a specific author cited. The latter problem no doubt results primarily from the authors' efforts to keep the

information as current and accurate as possible until time to go to press. After a second same-year publication by a given author is added, finding all the places that the first was cited previously would be a daunting task, although most should have been caught by a final, thorough, proof-reading. About 30 references cited in the text are not included in the reference list, at least under the date cited. Most of these probably represent mismatched dates, but at least three were omitted completely (Brewster 1893 cited on page 485; MacLean 1970 cited on page 128; and Southern 1958 cited on page 531). Authorship of *The Birds of Alberta* editions is garbled. The 1966 edition, revised by W. R. Salt, was published under the authorship of Salt and Wilk, not W. R. and J. R. Salt, while the 1976 book was authored by W. R. and J. R. Salt, not W. R. alone. I was able to detect only a few errors of a substantive nature. Although "most" accurately describes the British Columbia proportion of the breeding populations of most of the species listed on page 11, I believe that breeding populations in other provinces of Western Wood-Pewee, Warbling Vireo, House Finch, and Red Crossbill are sufficiently large that "most" would be somewhat overstated. The text statement (page 62) that Dusky Flycatcher has been reported only once on Vancouver Island contradicts the accompanying map (page 63) on which two Vancouver Island locations are plotted, and the list of noteworthy records (page 67), where two records are included. Although Bewick's Wren has nested in southern Ontario (page 310), nesting there is not regular and probably has not occurred since the late 1950s. Examination by National Museum of Canada [now Canadian Museum of Nature] personnel showed that the purported Veery specimen collected on 20 May 1893 in Victoria (page 389) was in fact a Swainson's Thrush (D. R. Gray *in* M. K. McNicholl, 1978. Murrelet 59: 102–104).

The four-letter codes listed for each species are somewhat problematical. If such a list of codes is to be useful, the same codes should be used by all observers and the codes should be stable. Besides the obvious problem that some codes could logically refer to two species (e.g. is BASW Barn Swallow or Bank Swallow?; is CEWA Cedar Waxwing or Cerulean Warbler?), some of the codes also change every time that the American Ornithologists' Union publishes a list of name changes (approximately every two years). To test the usefulness of the codes, I compared those in this book with those for the same species published the same year by Peter Pyle in *Identification Guide to North American Birds. Part I,* Slate Creek Press, Bolinas, California. The codes in Pyle's book are those considered official in 1997 by the Canadian and U.S. banding authorities. Although most codes in the two books are identical, those for 12 species (Western Wood-Pewee, Gray Kingbird, Tree Swallow, Bank Swallow, Barn Swallow, Gray Jay, Western Scrub-Jay, Canyon Wren, Cedar Waxwing, Northern Shrike, Yellow Wagtail, and Black-backed Wagtail) differed. Moreover, the code used for Canyon Wren in the British Columbia book is used for Cactus Wren by Pyle and the banding authorities, and the code for Black-backed Wagtail (BBWG) in Campbell's 1998 provincial list differs from the two codes used in the two books (BBWA and BWAG).

Its few errors do not detract from the overall high quality of this book. Every professional and amateur ornithologist and "birder" in British Columbia and adjacent areas should have copies of all three volumes as a basic information source on what is and is not known about the avifauna of this large and diverse province. We all wait for the fourth and final volume with eager anticipation.

MARTIN K. MCNICHOLL

4735 Canada Way, Burnaby, British Columbia V5G 1L3, Canada

A Guide to the Birds of the West Indies

By H. Raffeale, J. Wiley, O. Garrida, A. Keith, and J. Raffeale. 2000. Princeton University Press, Princeton, New Jersey. 511 pp., illus.

The real James Bond would be pleased. This book is an update to the original guide to the birds of the West Indies, published by Bond in 1936. Not only is it a revision of the Bond's book, it goes beyond the traditional concept of a field guide and adds some new and interesting dimensions.

Looking first at this book as a field guide. It covers 564 confirmed species, including five extinct birds. These animals are found on islands throughout the Caribbean, in a rough triangle from Grand Bahama to San Andrés and Granada. It does not include Trinidad, Tobago, Aruba, Cozumel, and a handful of smaller islands close to the South and Central American coasts.

All the species are shown in full colour in a series of plates painted by seven artists. There are generally

about eight to 12 species per page. As the book is slightly larger (16 × 24 cm or 6.25 × 9.5 inches) than a typical guide, the individual portraits are a respectable size. Opposite each plate are cryptic comments on the most significant field marks. The only black-and-white drawing is of bird topography.

The 86 plates are followed by a one third to half page description of the key identification features, status, range, and other relevant comments. A 4 × 2.5 or 3 cm range map accompanies each text section. The identification remarks cover all the key characteristics as needed for identifying a species in the field . Where appropriate this includes the difference between males, females, and immatures. Similar species are noted along with their essential differences. This includes species that might occur as vagrants (for example, American White Pelican and Eastern White and Pink-backed pelicans). When a species is distinctive this section is left out (e.g., Magnificent Frigatebird). Local common names are included for each island. This will help you identify at least the range of possibilities from information provided by local people. ("Gaulin" is used in several places and for several species of heron-egret).

The quality of the plates is splendid. I looked carefully throughout the book at the shape, posture, and details of coloration of the birds depicted. I could find nothing of any consequence. Far more often I was impressed to the point where I began making a comparison to the great Thorburn.

So as a field guide this book has it all: good up-to-date coverage, top quality plates, and crisp supporting text. Now we can look at the additional material provided by the authors.

The first, and most impressive, innovation is that they have repeated the illustrations of the island endemics on eight additional plates. So as well as finding the Hispaniolan Woodpecker on the woodpecker plate, you can also see a different rendition on the Hispaniolan endemics page. This brings a sharp focus to the species distribution on the individual islands. In addition, there are 12 plates depicting a single endemic species, such as the Martinique Oriole. These paintings frequently include a full or partial rendition of the bird's habitat. Such additions give the book an increased aesthetic appeal.

There is a survey of the conservation status and efforts on 19 of the major islands or island groups. Not surprisingly the level-of-effort and the effectiveness of the conservation programs varies widely. What was a surprise is which islands have an effective conservation effort and which need a greater effort. This section, as well as the introductory material, is well worth reading.

So what could I find wrong with this book; not much really. The distribution is defined on the maps by encircling the area with a line. This is not as visually effective as blacking in the land mass. My bias is to have the plates opposite the text in the style of the National Geographic guide. The limited descriptions opposite the plates are very cryptic. For example, for non-breeding Piping Plover it reads "Black bill"; for Semipalmated Plover it says "Dark bill." You have to turn over 200 pages to get more information from the species account. As I said it is hard to find serious fault with this great new guide to a popular tourist area.

I think 007 would also be happy. After all, it took five authors to replace the original Bond!

ROY JOHN

2193 Emard Crescent, Gloucester, Ontario K1J 6K5, Canada

A Guide to the Birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka, and the Maldives

Richard Grimmet, Carol Inskipp, and Tim Inskipp. 1999. Princeton University Press, Princeton, New Jersey. 888 pp., illus. U.S. $85.

Each year brings more great new birding books, but rarely are they as long awaited and as valuable as the *Birds of India*. Not surprisingly, and as befits one of the world's great centers of biological diversity, the Indian subcontinent is graced with a wealth of ornithological literature, including several useful field guides. However, up until now there has been no one book aimed at the bird watcher that pulls it all together in one neat package. Here it is.

All 1300 species found in the seven countries that form the region are covered in an astonishing 153 plates crafted by 12 well-known bird artists. All major forms are illustrated including both sexes, immatures, and subspecies as appropriate. Where necessary, multiple views are included to illustrate birds in flight or at various angles. Despite the large number of illustrations, most of the plates escape overcrowding; some are works of art (the green pigeons on plate 35 are stunning). Each plate has a facing page with a short narrative description of the species covered. All of the illustrations are labeled and referenced in the facing text.

The format of the book will be instantly familiar to anyone who owns any of the several regional

guides Princeton has released over the past few years; a short introductory section including a history of ornithology in the subcontinent, a description of the major habitat types, tips on how to use the book, followed by information on conservation. The species descriptions focus on identification and include sections on voice, habits, habitat, and breeding. Where appropriate, descriptions are broken down by sex, age, and subspecies. Each account includes a summary of the bird's status in each of the seven countries covered by the book. The range maps indicate breeding, wintering, and passage ranges for each species. The exhaustive research that went into the book is demonstrated in high quality of the text, range maps, and extensive references. The fact that many range maps include question marks reflects the challenges inherent in studying such a massive area and will doubtless inspire further fieldwork.

How good is this book? The plates and description of birds I know well are excellent; key features are accurately illustrated and described, and multiple views are provided of problematic species (e.g., raptors, lariids). The plates are on a par or surpass the quality of many top guides, for example, it has the best pictures of tropical terns I have seen in any (e.g., it pictures Sooty and Bridled Tern in heavy molt, and illustrates the pale secondary covert bar usually overlooked in drawings of Brown Noody). The recently released guide to the West Indies, also published by Princeton, has a total of three pictures of Sooty and Bridled Tern; *The Birds of India* has ten. Another good example: there is an excellent painting of a juvenile Temminck's Stint, clearly illustrating the diagnostic sub-terminal "anchor" markings in the mantle feathers. This attention to detail is maintained throughout the plates, including in the myriad drawings of "little brown jobs" with which the subcontinent is amply blessed — enough obscure chats, warblers, flycatchers, and wheatears to satisfy the most discriminating birder's palate.

Are there problems? Any book of this nature must make compromises. The challenge of handling over one thousand often very similar species means that luxuries such as the stand alone "hawks in flight" plates featured in many guides are left aside. Also, some readers may find the small text a bit of a challenge; occasionally the range maps are hard to make out, particularly the paler shading used to indicate wintering ranges. A few of the plates are overcrowded, 45 pictures of psittacula type parrots on one page is overwhelming. Additionally, the arrangement of birds is occasionally confusing to the eye, and it is often necessary to cross check the numbers against the facing text. While the color separation and detail on the plates is exceptionally good, many are set against a rather gloomy gray background which detracts from their visual impact. Many of the facing pages to the plates have large patches of empty space, which is a waste given the severe space constraints which faced the authors. I found no errors in the species accounts of birds, and the book is remarkably free of proof-reading errors.

Some sort of index to the plates would be helpful, particularly to rapidly locate some of the more complex groups. It should be noted that this is perhaps the first major field guide to reflect some of the recent major shuffling of taxonomic groupings, thus birds tend to show up in odd places (e.g., Grebes and Loons, former front runners, are at plate 75, about halfway through).

Should you buy this book? It is hard to imagine any birder who has caught the Asian birding bug not rushing to get it. But before you do, consider that it is a comprehensive reference work, not a field guide. At 888 pages and 2.5 kilos you cannot casually slip it into your pocket. Fortunately, and following a precedent set in earlier Princeton tomes, a slimmed down, low budget, field guide version consisting primarily of the plates is available, and I suspect that this is the version that most travelers will want to use.

Is a bird book on the Indian subcontinent relevant to Canada? Oddly enough, yes. The treatment of Asiatic migrants is so good that is bound to become a critically important reference for anyone interested in vagrants. You don't have to be a hard core birder to admire this handsome book; it would make a great addition to any natural history library.

MARK GAWN

Canadian High Commission, P.O. Box 404, Bridgetown, Barbados, West Indies

Trogons and Quetzals of the World

By Paul A. Johnsgard. 2000. Smithsonian Institution Press, Washington. xi + 223 pp., illus. U.S. $49.95.

In the introduction, the author singles out one trogon, the Resplendent Quetzal as the "ultimate symbol of beauty." This is how many birders and I think of this entire group of birds. He begins the actual text with "Trogons ... (are).. characterized by unique toe arrangement." and, at first, this seems to me an odd way to view these colourful species. But, as you read through the taxonomy then this introduction makes sense. In fact this early statement sets the tone for this book. For while this is a book for all of those who are interested in tropical birds it is clearly written by a scientist with a scientific viewpoint. The author routinely uses terms such as rectrices and maxilla instead of the more common tail feathers or top of the bill. This is not a major problem if readers are willing to use the thoughtfully written glossary at the back of the book.

The book covers the currently recognized 39 species of trogons. It begins with the comparative biology, which includes an absorbing account of trogon evolutionary development. The species accounts include a description of range, size statistics, and the plumage of males and females as adults and juveniles. The notes on identification both in the field and the hand are helpful to birders and scientists. These accounts are rounded out with sections on ecology, behaviour, breeding biology, and conservation. A distribution map is also included. Please note this is not, nor is it intended to be, a field guide.

These species accounts are as detailed as possible given the current level of information. The author has rendered the birding and science communities a great service by pulling all this information in a coherent, readable form. What is very noticeable in these accounts is how many times there is little or no information available. Even such simple data as the typical number and colour of the eggs is unknown for several species. This means that amateurs and the growing number of ecotourists can make a singular contribution if they find and carefully document any trogon nest, and then send this information to the author.

The birds are primarily illustrated with plates by Gould. These plates were originally used in the last book on trogons published in about 1838. The illustrations are delightfully Victorian, showing birds in a setting of orchids, bromeliads and other tropical vegetation. As identifying tools they lack much of the clarity of current illustration techniques, but as this book is not meant to be a field guide I do not see this as an issue. Each distribution map is accompanied by a line drawing of a male bird. While the drawings are sound, they lose much in being black-and-white. For example, the Violaceous (a blue-and-yellow bird) and Collared Trogons (a green-and-red bird) look identical in black-and-white whereas they are very different in reality.

The author has added two sections I found most interesting. He has produced a key; much like those used in flower guides, for separating the species. This could be useful, especially with birds seen only partially because of the forest cover. He also defines the meaning and origin of the scientific names. To those of us who never studied Latin or Greek this adds a helpful clarification.

I think this book is first an important contribution to bird literature, second an interesting and readable account of an astounding group of birds, and third, I hope, an inspiration to birders to record their observations. However, I did find some silly errors. Figure 6, for example, is wrong. It is obviously Figure 5 repeated with the heading changed. I suspect the real Figure 6 lies buried in the printer's cupboard.

The author states that Gould's illustrations, being painted from museum specimens, are not completely accurate. When I looked at the plate for the Blue-tailed Trogon, a species I have not seen, I decided to verify the bird's appearance against the description. Looking up the species in the index, I turned to the pages indicated and found the description was at odds with the plate. I searched my library and located another illustration that supported Gould's version of the bird. After a period of confusion, I realized the index was in error (It had led me to the Black-tailed Trogon). I did a sampling of the rest of the index and did not find another problem. Later, however, I discovered the Surucua Trogon is listed as plate 26 when it is plate 27. So be careful how you use the index.

Despite this lapse of detail, this book is worth buying for several reasons. It will be valuable to the growing number of North Americans visiting South and Central America. The book will delight those who like attractive bird books. After all it will cost you about $20,000 U.S. to buy Gould's original. It opens a path for enthusiastic amateurs and professionals to contribute to our knowledge. Hopefully it will also spur the process of conservation of the rapidly diminishing rain forest.

ROY JOHN

2193 Emard Crescent, Gloucester, Ontario K1J 6K5, Canada

Research and Management of the Brown-headed Cowbird in Western Landscapes

Edited by M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich. Studies in Avian Biology #18. Cooper Ornithological Society. 312 pp. U.S. $18.00.

The Brown-headed Cowbird, once appropriately known as the Buffalo-bird, initially occupied a range similar to that of the American Bison. As agriculture advanced, for example as clearings appeared in forests, cowbirds expanded their range to cause adverse effects on many species including the Kirtland's Warbler in Michigan. A conference held in Sacramento, California, 23-25 October 1997, involved almost all experts in the field, and included papers on cowbird ecology, cowbird management, and cowbird control.

An overview essay precedes each of the three sections. Scott Robinson, University of Illinois, summarizes the 12 papers reporting factors affecting the abundance and distribution of cowbirds. James N. M. Smith, University of British Columbia, reviews the 15 papers dealing with host selection, impact on hosts, and criteria for taking management action. Linnea S. Hall and Stephen I. Rothstein give an overview of the five papers dealing with the efficacy of control and proposed alternatives to standard control practices.

The reader quickly becomes aware of the prodigious amount of effort represented by these papers; several individual studies involved over 100 observers and innumerable hours of field studies and desk analysis. In monetary terms, a million dollars a year is spent annually trapping cowbirds in California.

Habitat remains extremely important. Some wilderness areas in Idaho have no cowbirds at all; farther south, in the Sierra Nevada, cowbirds are progressively less common at higher elevations. In Coastal Sage Scrub in California, only 3 of 217 nests were parasitized. Common Yellowthroats had lower parasitism and predation rates and higher nesting success when they nested in extensive cattail marshes. Western species, especially Sage Sparrows, Horned Larks, and Western Meadowlarks, largely avoid parasitism because cowbirds arrive after initiation of their nests. Scarcity of observation perches in shrub-steppe areas also tends to decrease parasitism. Cowbird abundance is strongly influenced by distance to cattle; most cowbird flights are less than 3 km; cowbirds are usually absent 7 km from feeding areas. Rotation of livestock away from host breeding habitat thus becomes a promising management tool.

Smith's overview suggests that cowbird management programs are indicated when over 60% of nests are parasitized, and rarely indicated when nest parasitism rates are below 30%. However, Lazuli Bunting populations are not sustainable when parasitism rates exceed 20%, because 90% of Lazuli Bunting nests that fledged a cowbird chick did not fledge a single bunting chick. Similarly, 75% of southwestern Willow Flycatcher nests failed when parasitized. Up to 43% of nests of the endangered Least Bell's Vireo were parasitized at least once; removal of cowbird eggs, a labour-intensive exercise, increased annual productivity by up to 44%. In British Columbia, where Song Sparrows experienced intense parasitism and frequent nest failure, cowbird egg removal sharply lowered sparrow nest failure rates.

It is difficult to collect data on the fecundity of individual cowbirds, but they appear to lay between 1.72 and 8.16 eggs per female. Some cowbird females lay each egg in the nest of a different host species.

When one prolongs the study period, adverse effects of cowbird parasitism are more severe than most short-term studies of nests alone would indicate. Survivorship studies to four weeks post-hatching found that hosts often restrict their feeding to the larger cowbird, allowing their own young to starve. Thus, Indigo Buntings are only 18% as likely to return the next year if they fledge from a nest that contains a cowbird. Survivors in other species may have lower fecundity later in life.

What management tools are effective? Prescribed burning in southern Wisconsin lowered parasitism of Red-winged Blackbirds. In pastures with high cattle concentration at the Fort Hood military installation, Texas, initial Black-capped Vireo parasitism rates were 91%. Cowbird trapping, especially in pastures with high cowbird concentrations, reduced this rate.

Next, removal of cattle from one area led to a decline in cowbird parasitism of Black-capped Vireos from 35% one year to zero the next year. With all control measures combined, this vireo parasitism rate fell to below 9%. In central California, cowbird trapping decreased the parasitism rate on Willow Flycatchers from 65% to 39% and the number of flycatchers fledged per female increased from 1.04 to 1.72.

Items cited above are merely representative of the myriad of new and interesting facts gleaned from a well-planned, well-organized, well-reported, state-of-the-art conference.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8, Canada

Owls: A Guide to the Owls of the World

By Claus König, Friedhelm Weick, and Jan-Hendrik Becking. 1999. Yale University Press, New Haven CT. 462 pp., 64 colour plates.

This is a beautiful, impressive book with major flaws. Apart from its aesthetic value, if you already own *Burton's Owls of the World* (1973), do you need to buy this new book?

With a combined wealth of experience, König and Becking present 212 species of owls, worldwide, a remarkable increase from the 133 species listed by Burton in 1973. Many island taxa, considered subspecies by previous authorities, especially James L. Peters in volume 4 of his *Birds of the World*, have been elevated by König and Becking to full species status. Differences in vocalisations, even though some of these "may be barely distinguishable to the human ear," have played a role in these decisions, which still await further elaboration in peer-reviewed journals. For example, in the genus *Tyto* this book lists 17 species versus 8 in Burton; in *Otus*, 67 versus 34.

The hero of this book is Weick, who has 402 individual paintings of owls in 64 colour plates, 7 to 16 per plate. Many species are also depicted in flight and in downy (mesoptile) plumage. In addition, Weick has contributed 49 appropriate and attractive black-and-white sketches throughout the introductory text. This is a prodigious achievement, far surpassing the 80 paintings in Burton's book, — though Burton had coloured photographs and this book has none.

There is a succinct 19-page overview of owls, their specialized anatomy, then Topography, Food, Hunting, Behavior, Breeding, Vocalisations, and Systematics and Taxonomy. As a somewhat unconnected interpolation, Michael Wink and Petra Heidrich offer a 19-page account of molecular evolution and systematics, too technical for the average reader and perhaps too radical for some specialists.

Beyond the 64 plates, the remaining 240 pages are devoted to species accounts, roughly one page per taxon. Each species account is illustrated by one map, with helpful arrows pointing to individual islands where local forms exist. The strongest feature is the emphasis on vocalisations.

Although the authors acknowledge assistance from experts in six major museums and universities in North America, I doubt that any of them read the species accounts, or advised on appropriate North American reference sources, which are grossly under-represented. (This may represent poetic justice for generations of North American authors who have ignored important European sources). I will offer five examples, the first three concerning the Great Horned Owl:

(1) The error of naming the pale, northern subspecies, *Bubo virginianus wapacuthu*, is perpetuated, although Browning and Banks have shown conclusively that the initial specimen given this name was a Snowy Owl. (2) The statement "weighs about 1000 g," although even males average more than this throughout most of the range, and a female may reach 2500 g. (3) The contention, "has to be considered endangered in some regions," when in fact is it one of the most adaptable and successful of owls anywhere. (4) It is not true that "even the palest individuals" of the Great Horned Owl are "much darker than" the Snowy Owl. (5) The Barred Owl is said to be "expanding its range on the Atlantic side of North America, where it now overlaps with that of the Spotted Owl," whereas Pacific side is the case.

For a text that claims to emphasize the importance of vocalisations and behaviour, I was disappointed in a number of accounts. For example, the repetitive, regularly repeated whistle of the Northern Saw-whet Owl is poorly described as a "toot," and the remarkable injury-feigning of some Long-eared Owl adults near the nest is not mentioned.

Occasionally, the text contradicts the map (e.g., Western Screech Owl map and Oaxaca Screech Owl text). Some taxonomic decisions were admittedly made on remarkably little evidence (e.g., moving the Itombwe Owl into the genus *Tyto*). Available longevity records from bird banding have been ignored.

In summary, the illustrations are the main reason for purchasing this book, even for some who already own the Burton book. However, those interested only in North American owls are advised to buy the more accurate and informative *North American Owls* by Johnsgard; I understand a new edition of Johnsgard is in preparation.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8, Canada

A Field Guide to Reptiles and Amphibians of Eastern and Central North America

By Roger Conant and Joseph T. Collins. 1998. Third Edition, Expanded. Houghton Mifflin Company, Boston. xviii + 616 pages. illus. $29.95. Distributed in Canada by Thomas Allen & Son, Markham, Ontario.

This attractive printing of THE classic eastern North American amphibian and reptile guide has a brash new cover with a composite of illustrations from the book: Red Salamander, Barking Treefrog, Green Iguana (lizard), Milk and King snakes, and Western Painted Turtle, and a line drawing of a generalized tadpole and its mouthparts, thus readily distinguishing it from the original third edition which appeared in 1991 (reviewed in *The Canadian Field-Naturalist* 105(4): 608-610) with a cover featuring only a single Pine Barrens Treefrog. But do not be mislead by the redesigned exterior or the epithet "expanded" attached to this bulky new version. True, it is bigger, "expanded" from xx and 450 pages to 616 pages, but the reader would search in vain for new information. The accounts apparently remain word-for-word from those of 1991, and the introductory sections and content of distribution maps are similarly unaltered. What makes it a "new" book to the publisher is the resetting of the type, the addition to some accounts of individual colour photographs, and the text placement of distribution maps in eye-arresting bold primary colours, red, blue, yellow, etc., to distinguish the ranges of subspecies instead of the variations of black-and-white hatching and spotting of the previous editions.

The classic comparative Peterson format, which stamped the series as unique and made it an outstanding success, grouped illustrations of similar species together in equivalent postures with diagnostic marks indicated by bars. Although these plates are retained together as a front section, they are deemphasized by the addition of the largely redundant new text photographs of animals in varied postures. Also regrettable is that the ease of comparison of grouped maps of earlier editions is lost. Maps only appear with text on individual taxa. No explanations or justifications for these innovations are given nor any indication that either author, especially, the senior one with this long experience in the functional importance of this guide, had any hand or say in the new design. This, presumably, is a product of a production staff with more of an eye for picture books than field-useful tools.

Field naturalists may still prefer to search out a copy of the 1991 edition. It has identical information in significantly less bulk, an important factor in a volume to be actually taken on outings. Armchair naturalists may, however, find more visual appeal in the new colourful "expanded" edition.

FRANCIS R. COOK

Researcher Emeritus, Canadian Museum of Nature, Ottawa, Ontario K1P 6P4, Canada

ENVIRONMENT

Acts of Balance: Profits, People and Place

Grant Copeland. 1999. New Society Publishers, Gabriola Island. 163 pp., illus. $17.95.

In Canada we are repeatedly being told future success relies on increased globalization. Also, in order for Canadians to compete bigger is better, or so our financial institutes argue. But is this true in all cases? Grant Copeland provides a look at mainly British Columbia cases with which he has been involved over the length of his career. These case studies suggest for communities, local and small are the more beneficial and successful enterprises. A balance between economics and ecology must be determined by society which according to Copeland can be achieved within the existing infrastructure only slowly and with great frustration.

Copeland states in the first chapter that the main purpose of the book is to offer examples of how we can live more environmentally sound and socially appropriate and thus preserve our cultural and ecological diversity. The author divides the book into six parts covering economics, quality of life, cultural diversity, integration of global with local, and government. All sections of the book rely heavily on Copeland's working experience. References are provided. The majority of the references are reports from boards, government, and consultants cited within the text. The layout on the whole is logical and highly readable.

This book, which would be of benefit to many in positions of authority, provides, if nothing else, an alternative to present economic thinking. Individuals fighting for community survival would do well to read the book to gain insight for potential solutions. I would also recommend the book to the general reader as educational reading. My copy contains several highlighted points for future reference.

M. P. SCHELLENBERG

434 4th Ave SE, Swift Current, Saskatchewan S9H 3M1, Canada

MISCELLANEOUS

Linnaeus: Nature and Nation

By Lisbet Koerner. 1999. Harvard University Press, Cambridge, Massachusetts. 298 pp., illus. U.S.$39.95.

Koerner combines her biography of Carl Linnaeus, 1707-1778, with "a case study of the relation between natural knowledge and political economy." Raised in a pastor's home, Linnaeus committed the book of Genesis to memory. "He regarded nature as the revealed works of God in space." Daily he read Latin, particularly Ovid and Virgil. His nature writings were "beautiful ... part rhapsody, part oral epic, part elegy, and part pericope exegesis." As Erasmus Darwin said, Linnaeus "may be said to have formed a language..."

Linnaeus built his botanical nomenclature upon the foundations of Aristotle, John Ray, Joseph Pitton de Tournefort, and Sébastien Vaillant. His legacy is the universally-used classification system of plants and animals. Koerner praises its practicality, simplicity, its appeal to both learned men and novices, and hence its usefulness.

In 1738, Linnaeus began his career as a medical doctor in private practice in Stockholm, specializing in the treatment of venereal disease, especially common among French courtiers. Such expertise may have helped his appointment as chief physician to the Swedish navy the next year. He was apparently the first to describe "miner's lung," contributed to knowledge about diet and nutrition, described battered children in 1752, and noted the serenity of well-swaddled Sami infants. In 1741 he moved back to his alma mater, Uppsala University, as professor of medicine. A year later he traded chairs to become professor of botany.

Linnaeus was a complex man. Given his achievements, his egotism was warranted. "No one," he said proudly, "has so totally reformed an entire science." His moods swung from euphoria to melancholia. Today he would be labelled as at least a cyclothymic personality, perhaps as a full-blown manic depressive. His enthusiasm was infectious; up to 300 people would attend the public nature walks he led twice a week. "A man of charisma and drive," he was noted for his intelligence and charm.

Linnaeus supervised, and usually wrote, 186 student dissertations. These disciples collected specimens for him throughout the known world; their voyages are depicted graphically on a world map. Thirty of their lives are summarized in Appendix B; five of them died abroad, including the two considered by Koerner to have been his most brilliant disciples, Pehr Löfling, who died in Venezuela, and Pehr Forsskål, who died in Yemen before he could take up his post as professor of botany. Among the survivors, Daniel Solander and Anders Sparrman circumnavigated the world with Captain Cook on his first and second voyages, respectively; Pehr Kalm spent over three years in America; Johan Peter Falck explored Russia; Carl Peter Thunberg was the first naturalist to visit Japan, where his memory is still revered. Their collections allowed Linnaeus to develop latitudinal, global, and alpine acclimatization theories, and to conceptualize the earth as a self-regulating superorganism (a precursor of the Gaia theory!).

Linnaeus hoped to reproduce the economy of empire and colony within Sweden by growing colonial cash crops in the north. Increased productivity would thus replace former territorial conquest as a means for Sweden to prosper. Such attempts to use science to stimulate the economy failed.

He grossly underestimated the number of plants and animals present in the world. About 10,000 plants had been named; he guessed that only another 10,000 remained undescribed, and that most should be tabulated in his lifetime. Once his *Species Plantarum* was published in 1753, one could, as Linnaeus proudly said, name plants "as easily as one names a person ... easy to remember, easy to say and write." *Systema Naturae* in 1758 did the same for the animal kingdom. His classification of humans as *Homo sapiens* (after toying with the alternate name of *Homo diurnus*) was "original in the realm of scientific thinking." Somewhat ambivalent, he said that "humankind was put here as a guest," yet that nature was created for man.

Linnaeus wrote anonymous but glowing reviews of his own publications in Stockholm newspapers; he padded his expense accounts. But he was generous with food to the hungry, especially starving mothers and children.

Petrus Artedi, Linnaeus' fellow botanist and best friend, drowned in an Amsterdam canal at age 30, after a party. Koerner omits mention that Linnaeus rescued the landmark ichthyology classifications of Artedi and published them three years posthumously. Throughout much of this biography, she offers a somewhat off-putting stress on "cameralism," (the theoretical elaboration of fiscal and economic governance), the central theme of her thesis and the title of a 1909 economics history book.

In the 1880s, Sweden was the source of mass emigration, losing one percent of its population each year to America. Associated with conservative thinking, the Linnaeus name was almost forgotten by the post-war social democratic government in Sweden. The Linnaeus Day holiday was cancelled. The 250th anniversary of his birth went almost unnoticed. He dwindled into a local hero.

Koerner's fascinating book, based on her Harvard

University dissertation, is highly recommended. Appendix A, a chronology, is a useful reference source. Appendix B, biographical references, was to me worth the price of the book. There are 48 pages of detailed footnotes and 19 pages of references. Unfortunately the names mentioned in the biographical references are not cited in the otherwise useful index.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8

NEW TITLES

Zoology

*__Albatrosses.__ 2000. By W. L. N. Tickell. Yale University Press, New Haven. 448 pp., illus. + 52 plates. U.S. $60.

__Annotated bibliography of quarternary vertebrates of North America.__ 2001. By C. R. Harington. University of Toronto Press, Toronto. c360 pp., $120.

__The bird almanac: the ultimate guide to essential facts and figures of the world's birds.__ 1999. By D. M. Bird. Firefly, Willowdale, Ontario. xvii + 460 pp., illus. $19.95.

†__The archaeology of animal bones.__ 2000. By T. O'Connor. Texas A & M University Press, College Station. 244 pp., illus. U.S. $ 34.95.

*__Biology of plethodontid salamanders.__ 2000. Edited by B. C. Bruce, R. G. Jaeger, and L. D. Houck. Kluwer/Academic Press/Plenum, New York. xiii + 485 pp., illus. U.S. $195.

†__Bird census techniques.__ 2000. By C. J. Bibby, N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2nd edition. Academic Press, San Diego. xvii + 302 pp., illus.

*__Birds of Europe.__ 2000. By K. Mullarney, L. Svensson, D. Zetterstrom, and P. J. Grant. Princeton University Press, Princeton. 400 pp., illus. Cloth U.S. $39.50: paper U.S. $29.95.

*__Birds of the World: a checklist.__ 2000. By J. F. Clements. Ibis Publishing, Vista, California. xx + 867 pp., U.S. $39.95.

__Birds of Nepal.__ 2000. By R. Grimmett, C. Inskipp, and T. Inskipp. Princeton Field Guides. Princeton University Press, Princeton. 288 pp., illus. U.S. $29.95.

__Bugs of Alberta.__ 2000. By J. Acron. Lone Pine Publishing, Edmonton. 160 pp., illus. $14.95.

†__Checklist of the birds of northern South America.__ 2000. By C. Rodner, M. Lentino, and R. Restall. Yale University Press, New Haven. 136 pp., U.S. $23.50.

†__Conservation priorities for the amphibians and reptiles of Canada.__ 2000. By D. Seburn and C. Seburn. World Wildlife Fund Canada and Canadian Amphibian and Reptile Conservation Network, WWF, Toronto. 92 pp., Free PDF copies available at www.wwfcanada.org (library)

*__Cuckoos, cowbirds, and other cheats.__ 2000. By N. B. Davies. Poyser, London, England. ix + 310 pp., illus.

*__A field guide to birds of the Indian subcontinent.__ 2000. By K. Kazmierezak. Yale University Press, New Haven. 352 pp., illus. + map. U.S. $32.50.

__Fire ants.__ 2000. By S. W. Taber. Texas A & M University Press, College Station. 368 pp., illus. U.S. $29.95.

*__Fossil snakes of North America: origin, evolution, distribution, paleoecology.__ 2000. By J. A. Holman. Indiana University Press, Bloomington, xi + 357 pp., illus. + plates. U.S. $ 69.95.

*__Gatherings of angels: migrating birds and their ecology.__ 1999. Edited by K. P. Able. Comstock Books, Cornell University Press, Ithaca. xi + 193 pp., illus. U.S. $29.95.

*__A field guide to the birds of India, Pakistan, Nepal, Bangladesh, Bhutan, Sri Lanka, and the Maldives.__ 1999. By R. Grimmett, C. Inskipp, and T. Inskipp. Princeton University Press, Princeton. 888 pp., illus.

†__Heron Conservation.__ 2000. Edited by J. A. Kushlan and H. Hafner. Academic Press, San Diego. xvi + 480 pp., illus.

__Islands of hope: lessons from North America's great wildlife sanctuaries.__ 1999. By P. Manning. John F. Blair, Winston-Salem, North Carolina. 211 pp., illus. U.S. $15.95.

*__Kingbird highway.__ 2000. By K. Kaufman. Mariner Books, Houghton Mifflin, Wilmington, Massachusetts. 318 pp., illus. U.S. $13.

__Living on the wind: across the hemisphere with migratory birds.__ 1999. By S. Weidnesaul. North Point Press, New York. xii + 420 pp., illus. U.S. $26.

*__Manitoba birds.__ 2000. By A. Bezener and K. DeSmet. Lone Pine Publishing, Edmonton. 176 pp., illus. $17.95.

†__A manual for wildlife radio tagging.__ 2001. By R. E. Kenward. Academic Press, San Diego. x + 311 pp., illus.

*__The nature of frogs: amphibians with attitude.__ 2000. By H. Parsons. Greystone Press, Vancouver. 112 pp., illus. Cloth $34.95; paper $24.95.

†**The nature of great apes: our next of kin.** 2000. By M. A. Gilders. Greystone Press, Douglas and McIntire, Vancouver. vii + 104 pp., illus. $34.95.

*__Reproductive biology of bats.__ 2000. Edited by E. G. Crichton and P. H. Krutzsch. Academic Press, San Diego. xi + 510 pp., illus.

†**Research techniques in animal ecology: controversies and consequences.** 2000. Edited by L. Boitani and T. K. Fuller. Columbia University Press, New York. xxxii + 442 pp., illus. U.S. $32.

†**The return of the wolf: reflections on the future of wolves in the northeast.** 2000. Edited by J. Elder. University Press of New England, Hanover, New Hampshire. 175 pp. U.S. $24.95.

Shrikes and bush-shrikes, including wood-shrikes, helmet-shrikes, flycatcher-shrikes, philentomas, batises, and wattle-eyes. 2000. By T. Harris. Princeton University Press, Princeton. 392 pp., illus. U.S. $49.50.

*__Snipes of the western palearctic.__ 2000. By R. Rouxel. Eveil Nature, Saint Yrieux sur Charente, France. 304 pp., illus. English or French 215 FF.

†**Threatened birds of the world.** 2000. Edited by A. J. Stattersfield and D. R. Capper. Birdlife International and Lynx Edicions, Barcelona, Spain. xii + 852 pp., illus. U.S. $115.

*__Turtle conservation.__ 2000. Edited by M. W. Klemens. Smithsonian Institute Press, Washington. xv + 334 pp., illus. U.S. $ 57.75.

Botany

†**Bryophyte biology.** 2000. Edited by A. J. Shaw and B. Goffinet. Cambridge University Press, New York. x + 476 pp., illus. Cloth U.S. $100; paper U.S. $35.95.

†**Contemporary plant systematics.** 2000. By D. W. Woodland. 3rd edition. Andrews University Press, Berrien Springs, Michigan. xiv + 370 pp., illus. + photo CD. U.S. $64.95.

*__Food webs and container habitats: the natural history and ecology of phytotelmata.__ 2000. By R. L. Kitching. Cambridge University Press, New York. xiii + 431 pp., illus. U.S. $100.

†**Green plants: their origin and diversity.** 2000. By P. R. Bell and A. R. Hemsley. 2nd edition. Cambridge University Press, New York. 349 pp., illus. Cloth U.S. $90; paper U.S. $31.95.

†**Magical mushrooms, mischievous molds.** 1998. By G. W. Hudler. Princeton University Press, Princeton. xv + 248 pp., illus. U.S. $14.95.

*__Phycology.__ 1999. By R. E. Lee. 3rd edition. Cambridge University Press, New York. x + 614 pp., illus. Cloth U.S. $ 100; paper U.S. $44.95.

*__Spatial pattern analysis in plant ecology.__ 1999. By M. R. T. Dale. Cambridge University Press. New York. x + 326 pp., illus. Cloth U.S. $69.95; paper U.S. $35.95.

Trees: their natural history. 2000. by P. Thomas. Cambridge University Press, New York. x + 286 pp., illus. Cloth U.S. $64.95; paper U.S. $24.95. F

Environment

Don't breath the air: air pollution and U. S. environmental politics, 1945 – 1970. 2000. By S. H. Dewey. Texas A & M University Press, College Station. 336 pp. U.S. $39.95.

*__Fatal consumption: rethinking sustainable development.__ 2000. Edited by R. E. Woollard and A. S. Ostry. UBC Press, Vancouver. ix + 270 pp., illus. Cloth $75; paper $29.95.

†**The geometry of ecological interactions: simplifying spatial complexity.** 2000. Edited by U. Dieckmann, R. Law, and J. A. J. Metz. Cambridge University Press, New York. xiv + 565 pp., illus. U.S. $74.95.

†**The global environment in the twenty-first century: prospects for international co-operation.** 2000. Edited by P. S. Chasek. United Nations University Press, Tokyo. x + 465 pp., illus. U.S. $39.95.

*__Pandora's poison: chlorine, health, and a new environmental strategy.__ 2000. By J. Thornton. MIT Press, Cambridge. xii + 599 pp. U.S. $34.95.

*__Reading the entrails: an Alberta ecohistory.__ 1999. By N. C. Conrad University of Calgary Press, Calgary. xviii + 197 pp. $19.95.

*__Seasons of the Arctic.__ 2000. Photographs by P. Nicklen, text by H. Brody. Greystone Books, Vancouver. 128 pp. $45.

†**Simulating ecology and evolutionary systems in C.** 2000. By W. Wilson. Cambridge University Press, New York. xv + 301 pp., illus. Cloth U.S. $85; paper U.S. $29.95.

Small creatures and ordinary places: essays on nature. 2000. By A. M Young. University of Wisconsin Press, Madison. 288. pp., illus. Cloth U.S. $50; paper U.S. $19.95.

*__Something new under the sun: an environmental history of the twentieth century world.__ 2000. By J. R. McNeill. W. W. Norton, New York. ix + 421 pp., illus. U.S. $29.95.

†**Voices for the watershed: environmental issues in the Great Lakes – St. Lawrence Drainage Basin.** 2000. Edited by G. G. Beck and B. Littlejohn. McGill-Queen's University Press, Montreal. xiii + 299 pp., illus. $39.95.

†**Wetland ecology: principles and conservation.** 2000. By Paul A. Keddy. Cambridge University Press, New

York. xiv + 614 pp., illus. Cloth U.S. $140; paper U.S. $52.95.

Miscellaneous

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Editor: Dr. Francis R. Cook, R.R. 3, North Augusta, Ontario K0G 1R0; (613) 269-3211; e-mail: fcook@achilles.net
Copy Editor: Wanda J. Cook
Business Manager: William J. Cody, P.O. Box 35069, Westgate P.O. Ottawa, Canada K1Z 1A2 (613) 759-1374
Book Review Editor: Dr. J. Wilson Eedy, R.R. 1, Moffat, Ontario L0P 1J0; e-mail: edith@netcom.ca
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Cover: *Trillium ovatum* Pursh variety *hibbersonii* (Taylor et Szczawinski) Douglas et Pojar, variety nova. See note by George Douglas and Jim Pojar, page 343. Photo courtesy of George W. Douglas.

The Canadian Field-Naturalist

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Tiger Salamander, *Ambystoma tigrinum*, Movements and Mortality on the Trans-Canada Highway in Southwestern Alberta

Anthony P. Clevenger[1,2], Mike McIvor[3], Diane McIvor[3], Bryan Chruszcz[4] and Kari Gunson[4]

[1]Faculty of Environmental Design, University of Calgary, 2500 University Avenue, N.W., Calgary, Alberta T2N 1N4 Canada.
[2]Mailing address: 625 Fourth Street #3, Canmore, Alberta T1W 2G7 Canada
[3]Box 1693, Banff, Alberta T0L 0C0 Canada
[4]Parks Canada, Box 900, Banff, Alberta T0L 0C0 Canada

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We report on the mid-season movements and mortality of Tiger Salamanders (*Ambystoma tigrinum*) along the Trans-Canada highway in Kananaskis Country, Alberta. The highway was surveyed for road-killed animals between April and November during 1997, 1998, and 1999. Road-killed Tiger Salamanders were collected on one day in 1998 and eight days in 1999. A minimum of 183 Tiger Salamander mortalities were recorded on a 1.05 km section of highway. The mean snout-to-vent length of eight road-killed salamanders was 103.1 cm. Movement was concentrated in one 300 m section of highway, primarily in one direction, and related to heavy rainfall events and warm weather. It was not clear whether movements were pre-breeding or post-breeding or why there was a sudden eruption in movements away from Chilver Lake.

Key Words: *Ambystoma tigrinum*, Tiger Salamander, migration, mortality, roads, Alberta.

The Tiger Salamander (*Ambystoma tigrinum*) is the most widely distributed amphibian in North America (Stebbins 1985). Populations commonly designated *Ambystoma t. melanostictum* are found in Canada in the province of Alberta south of Edmonton, from the eastern slope foothills to southern Saskatchewan and east to Manitoba (Stebbins 1985; Hooper 1992; Russell and Bauer 2000). Tiger Salamanders breed in shallow lakes, ponds, and backwaters in a wide array of habitats and are found at elevations of up to 2800 m (Petranka 1998). Over its entire North American range, the species breeds in almost every month of the year, depending on subspecies, geographic location, latitude and elevation (Petranka 1998), but mating in the northern latitudes generally occurs after early spring migration to breeding sites. Rarely seen in the open except during breeding season, Tiger Salamanders are primarily nocturnal and may be active from early spring to early autumn in Alberta.

Movement patterns of ambystomatid salamanders are particularly unclear since much of their post-transformation life is spent in subterranean burrows and most congregate only briefly at aquatic breeding sites (Duellman and Trueb 1986). Seasonal patterns of migration from terrestrial environments to breeding areas are well documented (Sever and Dineen 1978; Semlitsch 1985; Sexton et al. 1990), yet movements after the breeding season are poorly understood (Hairston 1987; Whiteman et al. 1994). In this paper we report on the spatial and temporal presumed post-breeding movements from road-killed Tiger Salamanders on a section of the Trans-Canada highway in Kananaskis Country, Alberta.

Study area and methods

The study area is in the Montane ecoregion and is composed of grasslands interspersed with forests of Lodgepole Pine (*Pinus contorta*), White Spruce (Picea glauca) and Aspen (*Populus tremuloides*). Situated in the Bow River Valley, the terrain has little topographic relief within the valley floor. A small pond and a lake (Chilver Lake) are located on the south side of the Trans-Canada highway, while another lake (Middle Lake) is on the north side of the highway (Figure 1). The distance between Chilver Lake and Middle Lake is approximately 1.7 km. Tiger Salamanders have been observed recently in all three water bodies (A. Clevenger, personal observation; H. Dempsey, personal communication). Earlier records of Tiger Salamander sightings in the Chilver Lake area were published by Salt (1979).

Between the months of April and November in 1997, 1998, and 1999, we systematically surveyed roads by vehicle in Banff National Park and adjacent Kananaskis Country, collecting data on road mortality of small and medium sized vertebrates. One of two routes surveyed the Trans-Canada highway from the Banff townsite to the junction of Highway 40. Surveys were alternated each day, commenced less than 1 hr after sunrise, and were conducted by two observers, one driving 10 km/hr below the posted speed limit, while the other searched for road-killed salamanders and other vertebrates on the road pavement. We observed road-killed Tiger Salamanders on the Trans-Canada highway west of the town of Seebe (51°04'N, 115°04'W; Figure 1) and 45 km east of the town of Banff on the following dates: 29 July 1998 at 0729 h (1 hr, 28 mins after sunrise), 11 August 1999 at 0724 h (56 mins after sunrise), 12 August 1999, 13 August 1999 at 0754 h (1 hr, 30 mins after sunrise), 14 August 1999, 15 August 1999, 30 August 1999 at 0745 h (55 mins after sunrise), 3 September 1999 at 0807 h (1 hr, 7 mins after sunrise), and 11 September 1999. The highway at the location of all road-kills was 43 m wide and consisted of four lanes of traffic, an open grass-covered median.

To assess whether road-killed salamanders were traveling in a specific direction we identified the high-kill concentrations on the eastbound and westbound lanes. Using the westernmost extent of road-kills on eastbound and westbound lanes as reference points we plotted the location of the remaining salamander road-kills. All points were obtained using a global positioning system unit and differentially-corrected (Trimble Navigation Ltd., Sunnyvale, California, USA). The distance from each road-killed salamander to the origin was recorded for all of the kills on both sides of the highway. These distances were used to add the salamander road-kills to an ArcView GIS point theme (Earth Systems Research Institute 1998). We described the spatial distribution of the salamander road-kills using spatial statistics software (Levine 1999). A cluster analysis was performed using the nearest-neighbor hierarchical clustering algorithm to determine where the majority of kills occurred in the eastbound and westbound lanes. An alpha value of 0.05 was used to locate clusters not produced by chance alone. We used a sample size of 92 (eastbound) and 19 (westbound) road-kills to produce a cluster. The mean center of each cluster was calculated and we ran a line between the two centers to approximate the direction the salamanders traveled as they moved across the highway.

Results and Discussion

Mortality

On the morning of 29 July 1998, we found and collected one road-killed Tiger Salamander in the westbound lane (north side) of the Trans-Canada highway west of the town of Seebe (Figure 1). The following year on the morning of 11 August 1999, we discovered a mass movement of Tiger Salamanders across the Trans-Canada highway at the same location as the single individual the year before. On this day we counted a total of 68 dead Tiger Salamanders on the highway. We collected only eight salamanders as most had been flattened and dismembered on the pavement. The total number of salamanders killed on the roadway was obviously much higher. While counting and removing the road-killed specimens from the pavement, we observed additional Tiger Salamanders approaching the road and unsuccessfully attempting to cross it. The following day (12 August 1999) we did not survey the highway but returned to the site and found two live Tiger Salamanders and estimated at least 50 or more dead on the highway pavement. On 13 August 1999 we carried out the survey and encountered 23 Tiger Salamanders killed on the Trans-Canada highway at the same location and noted that the salamanders were approaching the road and trying to cross it. The next day (14 August 1999) we did not survey the road but returned to the site and found one live salamander and estimated 20 or more dead on the road. On 15 August 1999 we found two dead Tiger Salamanders on the Trans-Canada highway, four that were several days old on a frontage road 25 m south of the highway and we found no salamanders live or dead while driving a two-lane road in Bow Valley Provincial Park situated 300 m north of the highway and parallel to it.

Two weeks later, on 30 August 1999, we counted a total of 18 Tiger Salamanders dead on the highway at the same location as previous road-kills. While dead specimens were being collected off the roadway live ones again were observed attempting to cross the busy highway. While conducting the survey on 3 September 1999 we counted one road-killed Tiger Salamander on the Trans-Canada highway at the same site as those recorded earlier. The final observation of salamander movement on the highway was on 11 September 1999 when one unsuccessfully attempted to cross the highway northbound.

The main pulses in Tiger Salamander movements across the Trans-Canada highway occurred during two distinct periods: 11–14 August 1999 ($n = 163$ mortalities) and on 30 August 1999 ($n = 20$). Overall we documented a minimum of 183 Tiger Salamander mortalities on the highway, all within a 1.05 km section, during a 30-day period.

At a rate of 24–40 vehicles/hour, Kuhn (1987) found that 50% of a cohort of migrating Common Toads (*Bufo bufo*) were killed. At 26 vehicles/hour the estimated road crossing survival rate of Common Toads was zero in another study (Heine 1987). The high traffic volumes on this section of the Trans-Canada highway during summer (mean daily traffic

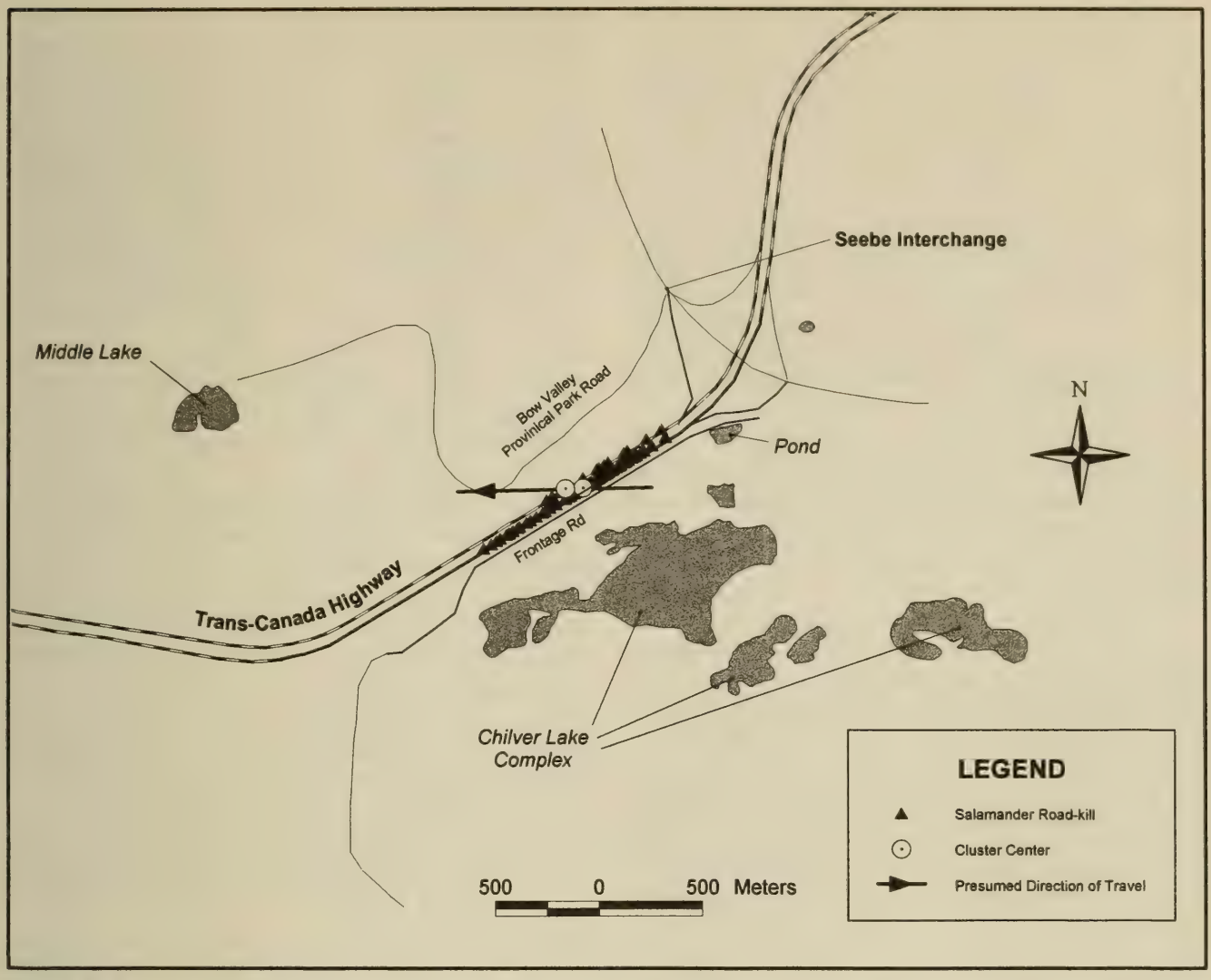

FIGURE 1. Location of Tiger Salamander road-kills along the Trans-Canada highway, Kananaskis Country, Alberta, Canada.

volume = 21 450 vehicles/day; Parks Canada Highway Service Centre, Calgary, Alberta) coupled with the slow movements of ambystomatids would result in exceedingly few individuals surviving the highway traverse. We were unable to document how many or what proportion of salamanders approaching the highway actually crossed safely.

We collected and measured the one specimen from 29 July 1998 and 7 of the 8 specimens collected on 11 August 1999. One individual was dismembered such that accurate measurements could not be made. The mean snout-to-vent (SVL) length of the eight salamanders was 103.1 cm (SD = 8.8), ranging from 90.0 cm to 120.0 cm. The sex of the individuals could not be determined externally. Based on the SVL the collected specimens appeared to be newly-transformed adults but none were dissected to determine either maturity or sex. We did not note any gill stubs that would have indicated transformation from larvae was just being completed as has been observed in some migrations elsewhere (F. R. Cook, personal communication).

Direction of travel and mortality distribution

In a similar report, Duellman (1954) found late-season eastern Tiger Salamanders moving randomly across a two-lane Michigan roadway; but he did not detect a definite migration in any one direction. The live Tiger Salamanders we observed approaching the highway were predominantly moving northbound across the Trans-Canada highway. We base this on our observations of Tiger Salamander movement and the high number of road-killed salamanders on the south side of the highway as opposed to the north side. During the first pulse (11–14 August 1999), we counted 73 (79%) of 92 road-killed salamanders on the south side, whereas 19 (21%) were picked up on the north side. Similarly, during the second pulse (30 August–3 September 1999) all 19 salamanders recovered were killed on the south side. Because we did not sample other areas peripheral to Chilver Lake, we cannot assume that salamanders only moved in the direction of the highway; they could have dispersed in many different directions from the lake. Nonetheless, the majority

of salamander movements appeared to originate from Chilver Lake.

Tiger Salamander kills were distributed on both sides of the highway for a distance of 1.05 km; however, most kills were concentrated in a 300 m section (Figure 1). Movement was concentrated in one localized area and primarily in one direction suggesting that seasonal migrations breeding or otherwise were occurring. Previous studies have reported that breeding and non-breeding season movements of Tiger Salamanders are triggered by environmental factors, in particular precipitation and temperature (Petranka 1998; Whiteman et al. 1996; Duellman and Trueb 1986; Fowler 1935). Pre-breeding movements would normally take place several months earlier and would have been detected during previous road surveys. Mid-season movement between ponds could explain the phenomenon, although it is unclear what triggered the salamanders to move during this one year and not in previous years.

The centers of road-kill clusters for east and westbound lanes were offset, indicating that salamanders were apparently crossing the highway at an oblique angle and not straight across. In Figure 1, the arrow implying the general direction of travel shows that movement was in the direction of Middle Lake, but not directly aligned. It was noteworthy that the greatest concentration of salamander movements across the Trans-Canada highway occurred at the highest point in the road and where the highway passed closest to Chilver Lake.

Weather

Although there is universal agreement that particular meteorological conditions elicit migratory behavior in Tiger Salamanders, few studies have noted what the specific ambient measures are, or tested their relationships with movements (Semlitsch 1983a; Duellman 1954). In South Carolina the number of migrating adult Eastern Tiger Salamanders (*Ambystoma tigrinum tigrinum*) was consistently correlated with total amount of daily precipitation, the amount of minimum daily rainfall amount being associated with movements was 13 mm (Semlitsch 1983a; Table 1). The minimum and maximum daily temperatures when more than 200 Eastern Tiger Salamanders were observed crossing a Michigan highway during autumn ranged from 5–9°C and 11–14°C, respectively (Duellman 1954). In our western study area, during the first and most important pulse in salamander movement across the Trans-Canada highway, 17 mm of precipitation fell in less than 24 hours and the minimum and maximum temperatures were 6.5°C and 17.0°C, respectively (University of Calgary Field Station, Kananaskis Country, Alberta).

We obtained the meteorological records for the years we observed Tiger Salamander movements (1998, 1999) and months they are found active (April to September inclusive). To further investigate weather effects we subjectively assigned a minimum amount of daily precipitation for salamander movement to be greater than or equal to 15 mm and minimum and maximum daily temperatures of at least 6°C and greater than or equal to 12°C, respectively (Table 1). We found in 1998 there were eight days with rainfall greater than 15 mm, but only three of those days (all in June) where the minimum and maximum daily temperature criteria were met. In 1999, 11 days had rainfall greater than or equal to 15 mm; however, only 3 of the 11 days had daily temperatures that matched our criteria. Of those three days, two coincided with Tiger Salamander migrations in the study area (10–11 and 30-31 August).

In 1999, we found Tiger Salamander movement to be related to heavy rainfall events and warm weather; however, the previous year there were favorable meteorological conditions for salamander movements but we did not detect any migration across the highway.

First, although we assume here that the movements we observed were post-breeding we cannot rule out late pre-breeding movements. Generally, in Alberta breeding occurs in early spring (Russell and Bauer 2000). However, at high elevation ponds in

TABLE 1. Meteorological conditions for Tiger Salamander migrations reported in the literature. Measurements in bold are minimal conditions in our study area when movements may be expected to occur.

Precipitation (mm)	Temperature minimum (°C)	Temperature maximum (°C)	Source
nr*	8.8	13.8	Duellman 1954
nr	5.0	11.1	Duellman 1954
13.4	nr	nr	Semlitsch 1983b
39.0	nr	nr	Semlitsch 1983b
16–18	5–8	11–13	This study
≥15	**≥6**	**≥12**	

*nr: not recorded.

Colorado and Utah breeding may be as late as July or August (Whiteman et al. 1995; Wissinger and Whiteman 1992; Worthylake and Hovingh 1989). At our study area favorable conditions providing opportunities for migrations in any given year or between years may be variable and few. Second, if the movements were post-breeding, the reason for the sudden eruption in movements away from Chilver Lake is unclear. They may have been moving to hibernation quarters (Hassinger et al. 1970; Fowler 1935) or moving between lakes as a result of density-dependent dispersal. There is some evidence to suggest that high density amphibian populations range widely for resources and when populations reach a density threshold large-scale dispersal events can occur (Langton 1989).

There is no detailed historical information published on Tiger Salamander movements in Alberta but Fowler (1935), writing from Aldersyde, noted local migration at the "harvest season". Patch and Stewart (1924) described a mass movement of Tiger Salamanders in Manitoba during later summer and autumn rainfall and similar movements have been observed in Saskatchewan and Manitoba (F. R. Cook, personal communication.)

Road mortality is thought to have significant negative effects on density of local amphibians (Ashley and Robinson 1996; Fahrig et al. 1995; Langton 1989). However, the level of threat from traffic to an amphibian population depends on a number of factors. The juxtaposition of ponds may or may not necessitate road crossing to access seasonal habitat. Some populations may be depressed through the added mortality presented by the road, while road mortality in other populations may have little impact (Langton 1989).

In order to assess the potential impacts of the Trans-Canada highway on the persistence of Tiger Salamander populations in this area, the regional conservation value of the existing ponds and lakes must be determined. Information on the Tiger Salamander distribution and degree of habitat connectivity in the area will help in understanding Tiger Salamander metapopulation structure and human impacts on it. At a local level, it will aid in assessing the significance of Chilver and Middle lakes for salamander persistence.

Proactive measures could be taken immediately to reduce road mortality of Tiger Salamanders in the study area by getting animals safely under the highway and still allow natural movements patterns. A 0.75 m diameter metal culvert is favorably located under the highway less than 50 m from the road-kill cluster centers, and in its present state, with temporary drift fencing, could be adapted seasonally for salamander passage. Tiger Salamanders usually are not philopatric to natal ponds and quickly colonize newly constructed ponds (Petranka 1998). Therefore measures to reduce mortality by creating new habitat on the Chilver Lake side of the highway to discourage cross-highway migrations might also prove effective at reducing salamander mortalities on the Trans-Canada highway.

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Possible Microclimate Benefits of Roost Site Selection in the Red Bat, *Lasiurus borealis*, in Mixed Mesophytic Forests of Kentucky

JEFFREY T. HUTCHINSON[1] and MICHAEL J. LACKI

Department of Forestry, University of Kentucky, Lexington, Kentucky 40546 USA
[1]Present address: Florida Department of Environmental Protection, Bureau of Parks, Hobe Sound, Florida 33455 USA

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Avoidance of diurnal predators is considered a primary selection factor influencing the choice of roosting sites by Red Bats (*Lasiurus borealis*), as this species is cryptically colored and difficult to observe in diurnal roosts. Other benefits to Red Bats resulting from choice of roosting sites, such as lowered energy expenditures due to more stable microclimates, have not been explored. We compared the thermal environment within diurnal roosting sites of Red Bats to other locations in the habitat where the bats would be potentially subject to fluctuations in temperature extremes. Data indicated that roosting sites of Red Bats had significantly lower overall average temperatures, overall variance in temperatures, average diurnal temperatures, and variance in diurnal temperatures than other locations in the habitat, with no difference observed for any nocturnal temperature variable. These results suggest that Red Bats roosting in forest habitats may gain a thermal advantage by selecting diurnal roosting sites that ameliorate variability and extremes in temperature.

Key Words: Red Bat, *Lasiurus borealis*, roosting habitat, temperature, Kentucky.

Environmental selection pressures important to the choice of roosting sites by forest-dwelling bats remain poorly understood (Brigham and Barclay 1996; Kalcounis and Brigham 1998). This is especially true for phytophilic bats; i.e., species that use the foliage of vegetation as roosting sites (Hutchinson and Lacki 2000). Bats that use ephemeral roosts, such as live trees and shrubs, switch roosts more frequently than species that occupy roosts that are predictable in time and space; e.g., caves and mines (Kunz 1982). Reasons purported to explain roost switching in foliage-roosting bats include decreased commuting costs to foraging areas, reduced predation pressures, and selection of alternate microclimates (Lewis 1995). Regardless, little data are available on how microclimate influences choice of roosting sites by phytophilic bats.

The Red Bat (*Lasiurus borealis*) selects roosting sites in the foliage of trees, shrubs, and vines (Barbour and Davis 1969; Shump and Shump 1982). Until recently, this species was believed to roost close to the ground along fencerows and forest edge (McClure 1942; Constantine 1959, 1966; Mumford 1973); however, more recent data obtained using radiotelemetric techniques demonstrated that this species also roosts high above the ground in the canopy of dominant trees in intact, second growth forest (Menzel et al. 1998; Hutchinson and Lacki 2000). As with other lasiurine species, the Red Bat is cryptically colored and blends in with furled, dead leaves. This trait has led several authors to postulate that cryptic coloration is an adaptation in Red Bats to minimize detection by diurnal predators while roosting in foliage (Orr 1950; McClure 1942; Constantine 1966). Hutchinson and Lacki (2000) discussed the relative merits of roost choice by Red Bats in relation to vulnerability to diurnal predators, and suggested that diurnal roosts selected high above the ground and away from forest edge should result in lower predation pressures.

Assuming predation pressure largely dictates diurnal roost site selection in Red Bats, it is still likely that additional factors could be a minor influence on choice of roosting sites. Constantine (1958) noted the effects of weather on roosting lasiurine species, including the Red Bat, and Watkins and Shump (in Shump and Shump 1982) observed that preferred roosting sites of Red Bats were associated with lowered evaporative water loss. Hutchinson and Lacki (2000) found Red Bats roosting exclusively in the shade in tree canopies, whereas others have observed Red Bats and other lasiurine species roosting in foliage but exposed to direct sunlight (Constantine 1958; Mumford 1973). This variability in roosting habits of Red Bats suggests that microclimate does influence roost site selection in Red Bats. In fact, based on his observations, Constantine (1966) listed vegetation that impedes wind currents, dust, and contributes to heat and humidity as an important factor in roost site selection of Red Bats. In this study, we measured temperatures within known diurnal roosting sites of Red Bats. We tested the null hypothesis that there is no difference in temperature conditions within Red Bat roosts compared to other, more exposed, locations in the habitat.

Methods

Roosting sites of Red Bats were located in the

Cumberland Plateau physiographic region of eastern Kentucky (Hutchinson and Lacki 2000). The area ranges 200–500 m in elevation and covers 28 500 km^2 of rugged, forested terrain (McGrain 1983). Forests are classified as mixed mesophytic (Braun 1950). Roosting sites were in second-growth hardwood forest that was largely undisturbed by silvicultural activities and contained mature stands of timber with an average dbh > 25.4 cm (P. Kalisz, University of Kentucky, personal communication). Dominant forest vegetation used as roosting sites by Red Bats were hickory (*Carya* spp.), Yellow-poplar (*Liriodendron tulipifera*), White Oak (*Quercus alba*), American Beech (*Fagus grandifolia*), and Chestnut Oak (*Q. prinus*), among others (Hutchinson and Lacki 2000).

Red Bats were radiotagged and tracked to roosting sites from May through August, 1996–1997. Methodology used in tagging and tracking Red Bats is outlined in Hutchinson and Lacki (2000). We located diurnal roosts in the canopies of trees using binoculars, and by lying beneath the roost tree 20–30 min before sunset and watching the bat emerge that evening to feed.

We placed temperature data loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA) in eight roost trees, in locations observed to be used as roosting sites by Red Bats. A more detailed description of roost sites of Red Bats examined in this study is available in Hutchinson and Lacki (2000). An additional eight data loggers were placed adjacent to or beneath the canopy of the roost trees in exposed settings for a paired comparison. An exposed setting was defined as a free air space > 10 m above ground that was not occupied or shielded by canopy foliage. We positioned data loggers in roosting sites and exposed sites using a slingshot, 18-kg fishing line, and a 56–85 g sinker. Once the line was in place, a data logger was tied to the end of the line and pulled up into position. This allowed data loggers to be directly situated in known roosting sites, while permitting data loggers in exposed sites to be placed as close to the same height off of the ground surface as possible. We periodically checked data loggers to ensure that their position was maintained.

Kunz and Nagy (1988) recommended the use of taxidermic mounts to house temperature sensors to more accurately measure operative temperature (T_e); thus, these data cannot be used to infer T_e. Because of the sample sizes involved and the likely damage to taxidermic mounts that could have occurred during this study, we were unable to make use of any existing museum collection. Regardless, given that taxidermic mounts still do not completely prevent bias in the data (Bakken and Kunz 1988), and that the approach we used required only a relative comparison, we suggest that the inferences made regarding differences in temperature conditions between roosting sites of Red Bats and exposed sites are valid.

Data loggers were operated for 42 days, from 13 July to 23 August 1997. We set data loggers to record temperatures ca. every 1.3 hr. We downloaded the data into Quattro Pro spreadsheets and tested data sets using 1-tailed, paired t-tests. We compared temperature conditions based on overall, diurnal, and nocturnal temperatures. In each case, we examined the average, minimum, maximum, and variance in temperature. To define diurnal and nocturnal temperatures, we divided the 24-h period based on local sunrise and sunset times. We hypothesized *a priori* that temperatures within roosting sites would be lower in average temperature, higher in minimum temperature, lower in maximum temperature, and smaller in variance in temperature.

Results

We observed differences between roosting sites and exposed sites for overall average temperature ($t = 2.57$, P = 0.025), average diurnal temperature ($t = 2.57$, P = 0.044), overall variance in temperature ($t = 2.02$, P = 0.014), and variance in diurnal temperature ($t = 2.81$, P = 0.013), with temperature conditions being less within roosting sites than in exposed sites (Table 1). We found no difference for any nocturnal temperature variable. Temperatures within roosting sites peaked at a lower level than exposed sites in midday, then dropped to levels inseparable between locations at night (Figure 1). These data indicate that roosting sites appeared to offer protection to Red Bats from the extremely high temperatures reached in midday, probably in part due to shading from direct solar radiation. Further, the low insulative capacity of vegetation likely explains the lack of a difference in temperatures within roosting sites and that of exposed sites during nocturnal hours.

Discussion

Red Bats in this area typically selected diurnal roosting sites high off of the ground in trees located on south-facing slopes on ridge tops of upland forests (Hutchinson and Lacki 2000). Hutchinson and Lacki (2000) argued that selection of roosting sites in these locations should result in lower exposure of Red Bats to diurnal predators. Regardless, these sites were more likely to receive a higher incidence of solar radiation than potential roosting habitats on north-facing slopes or at mid- and lower elevations. Red Bats did select locations within the roost trees under dense foliage near the outer canopy; thus, the vegetation probably shielded the bats from direct solar radiation during at least part of the midday sun. No Red Bat was ever observed in a roost directly exposed to solar radiation; however, Constantine (1958) suggested that lasiurine bats preferred west and southwest exposures to facilitate heating by the sun prior to emerging at dusk.

TABLE 1. Means and standard errors (SE) of temperatures (°C) within roosting sites of Red Bats, *Lasiurus borealis*, and exposed sites in the habitat in mixed mesophytic forests, Kentucky, 1997.

Temperature profile	Roosting sites Mean + SE	Exposed sites Mean + SE
Overall	23.59 ± 0.24[a]	24.34 ± 0.42
Minimum	8.44 ± 0.48	8.20 ± 0.40
Maximum	39.50 ± 1.20	42.74 ± 3.14
Variance	40.69 ± 3.87[a]	59.20 ± 5.93
Diurnal	27.68 ± 0.41[a]	29.26 ± 0.74
Minimum	15.52 ± 0.58	15.45 ± 0.45
Maximum	39.50 ± 1.20	42.74 ± 3.14
Variance	28.88 ± 3.17[a]	48.83 ± 6.36
Nocturnal	19.28 ± 0.19	19.23 ± 0.22
Minimum	8.44 ± 0.48	8.20 ± 0.40
Maximum	33.89 ± 1.92	34.29 ± 2.21
Variance	18.76 ± 2.45	20.22 ± 2.66

[a]Means within rows are different ($P < 0.05$).

Lewis (1995) proposed that foliage roosting bats have the benefit of alternative roosting sites and, because of greater roost site availability, have easy access to alternate roosting sites that offer different microclimates. Vaughan (1987) observed Yellow-winged Bats, *Lavia frons*, in Africa switching roost locations in accordance with temperatures, always choosing roosting sites in dense shade during the day in warm weather while moving to the open during cooler periods. Although the Red Bats in this area switched roosts frequently (about every 2.3 days; Hutchinson and Lacki 2000), they were most commonly observed in diurnal roosts motionless with their wings folded around their body. Others observed Red Bats in diurnal roosts in apparent torpor and also stretching and grooming (McClure 1942; Orr 1950; Mumford 1973).

Licht and Leitner (1967) suggested that reduced metabolic rates through inactivity appear to be important in reducing heat stress of bats in high temperatures. Tree bats are believed to maintain lower metabolism rates in order to conserve energy while in torpor when ambient temperatures are high (McNab1974). Torpor in bats was also demonstrated to be a strategy for water conservation, along with energy conservation (Herreid and Schmidt-Nielsen 1966). By maintaining themselves in a torpid-like state while in day roosts, we suggest that the Red

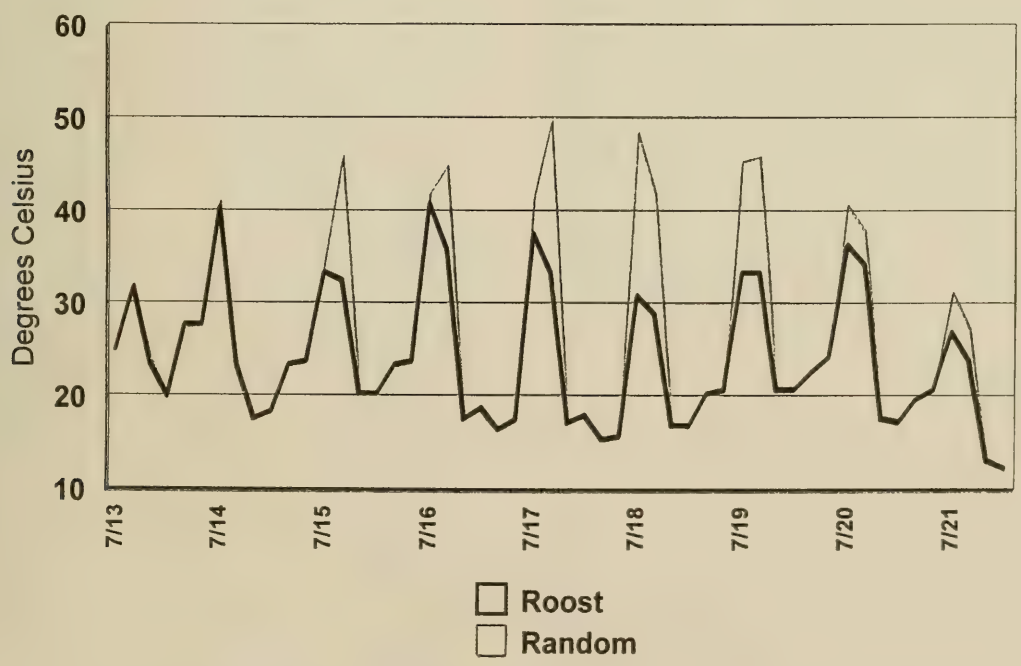

FIGURE 1. Temperature profile within a roosting site of a male Red Bat and a random exposed site during a nine-day period from 13–21 July 1997, in mixed mesophytic forest, Kentucky.

Bats observed in this study were behaving in a manner consistent with the above patterns.

Lasiurine bats are better insulated than other temperate-zone bats by having larger, thicker hair, and hair on the uropatagium. Greater insulation would enable these species to tolerate more air movement; i.e., draftier conditions, without concomitant changes in water balance and thermoregulation (Shump and Shump 1980). Canopy surfaces act to absorb wind and wind currents are normally stronger in the upper canopy than the forest floor (Nadkarni 1994). All roosting sites of Red Bats we discovered were near the top of the canopy, where wind currents were likely stronger than at mid-canopy or near the forest floor in a forest with a high percentage of canopy closure (Hutchinson and Lacki 2000). Temperature and relative humidity patterns vary inversely from the top of the canopy to the forest floor (Lee 1978; Parker 1995). During clear summer days, the temperature near the top of the canopy is higher and the relative humidity is lower, with these patterns reversed at the forest floor (Lee 1978). Our observations suggest that conditions under the canopy at ground level are stagnant and humid during the summer months in the deciduous forests of eastern Kentucky. Such conditions would result in added heat stress and water loss for Red Bats roosting at mid-canopy or below (Licht and Leitner 1967). In fragmented habitats, such as urban areas and farmland, canopy closure is lower because the vegetation is more widely spaced; thus, Red Bats would be more likely to select roosting sites lower to the ground (Constantine 1958, 1959, 1966; Mumford 1973), where wind currents aid in evaporative cooling during periods of high temperatures.

Most foliage roosting bats occur near the equator in tropical regions (Kunz 1982; Altringham 1997). Thus, the few species of foliage roosting bats that have distributions reaching into the Nearctic are likely to be subject to alternate selection pressures. One consequence of this is that most Nearctic foliage roosting bats are migratory, including the Red Bat (Shump and Shump 1982), to avoid climatic extremes in winter. We believe our data indicate that Red Bats are also sensitive to microclimate conditions during the summer maternity season.

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Ectoparasites in Lekking Sharp-tailed Grouse, *Tympanuchus phasianellus*

Leonard J. S. Tsuji[1], Jim D. Karagatzides[2], and Gerardo Deiluiis[3]

[1]Department of Environment and Resource Studies, University of Waterloo, Waterloo, Ontario N2L 3G1 Canada
[2]Department of Geography, Queen's University, Kingston, Ontario K7L 3N6 Canada
[3]Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5 Canada

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To investigate the validity of assumptions based on the parasite avoidance model, fifty-two male Sharp-tailed Grouse (*Tympanuchus phasianellus*) collected in northern Ontario from six separate leks were examined. Ectoparasitic burdens were recorded along with traits (feather damage, hematomas, body condition, body mass) and cues (territorial position, age) which may be used by the female to discriminate among males for their parasite loads. Neither assumption of the transmission avoidance model was met. Little variation in ectoparasite number existed in the breeding population as a whole or within individual leks. None of the traits or cues measured were correlated consistently with ectoparasitic burdens. These results suggest that randomly mating females would, on "average," mate with lightly infested individuals. Therefore, benefit to a discriminating female Sharp- tailed Grouse would be negligible.

Key Words: ectoparasites, lek, Sharp-tailed Grouse, *Tympanuchus phasianellus.*

A lek can be defined as an area used for mating, where males establish territories to form a cluster. Females visit the lek for the sole purpose of mating; resources on the lek (e.g., food) are limited. Although females have the opportunity to select any one of the males present as a mate, they often show unanimity in their choice of mate, selecting males occupying centrally located territories on the lek (Lumsden 1965; Kermott 1982). In this simple mating system, female mate-choice is theoretically based only on the benefits derived from the male himself.

The "parasite" or "transmission avoidance" model suggests that females prefer to mate with males with low ectoparasite numbers to reduce the probability of becoming infested (Borgia and Collis 1990; Clayton 1990). Two important assumptions of this model are that enough variation in ectoparasite number per male exists in the breeding population (and more specifically on individuals within a lek) to make mate choice worthwhile (Reynolds and Gross 1990), and that a trait or cue correlated with ectoparasitic burden facilitates choice. In this study, we determined if these assumptions of the transmission avoidance model are valid by examining individuals from leks of the Sharp-tailed Grouse (*Tympanuchus phasianellus*).

Methods

Study sites were located in areas of muskeg near Fort Albany (52°15'N; 81°35'W) in the James Bay Region of northern Ontario. One researcher accompanied several Native North Americans on their spring hunt for Sharp-tailed Grouse and examined birds shot before they were processed for food.

Fifty-two males were examined from six separate leks during the 1990–1992 breeding seasons. The numbers of birds obtained and the total numbers of males at each lek were as follows: lek 1, 2 of 22; lek 2, 12 of 15; lek 3, 8 of 17; lek 4, 4 of 12; lek 5, 16 of 19; and lek 6, 10 of 13. Leks 5 and 6 were observed for 12 days during the morning display period prior to collection to record copulations by individual males. Yearlings were differentiated from adults using the characteristic of feather-wear (Ammann 1944). Males were scored in the field, before they were collected, as occupying central vs. peripheral territories. Central territories were defined as those completely surrounded by other territories whereas peripheral territories were unbounded on at least one side (Kruijt and Hogan 1967).

Upon being shot, individuals were placed separately in plastic bags to prevent migration of ectoparasites between hosts (Eveleigh and Threlfall 1976). A feather-by-feather examination was conducted and ectoparasites were placed in 70 % alcohol for subsequent identification (Ash 1960; Eveleigh and Threlfall 1976). Feather damage was assessed for each specimen with individuals being placed in one of three categories: 0 (no damage to minimal); 1 (average damage); 2 (severe damage) [Clayton 1990]. Cervical apteria of each individual were assessed for presence or absence of hematomas (Johnson and Boyce 1989).

Individuals were weighed to the nearest 1.0 g using a spring scale or triple-beam balance. The physical condition of each male was assessed using an index based on the shape of pectoral muscle from keel to sternum (Macdonald 1962). Condition of males was classified as follows: 0, in good condition

(pectoral muscle distinctly convex and keel almost imperceptible); 1, in average condition (pectoral muscle flattened forming a planar surface between keel and thoracic ribs); 2, in poor condition (pectoral muscles concave and keel distinct). Spearman rank correlation analysis (r_s) was used to investigate the relationship between ectoparasite number and body mass among individuals of all leks.

Ectoparasite data, number of ectoparasites per individual, were pooled for all six leks and a frequency distribution was plotted. Frequency distributions, number of ectoparasites per individual, were constructed for individual leks at which more than 75% of males present on the lek were collected.

Data for ectoparasites were subjected to a Mann-Whitney U test between central and peripheral males for leks at which more than 75% of the males were examined and for all leks combined. In addition, ectoparasite data for all leks were subjected to a Mann-Whitney U test to determine whether adults and yearlings differed.

Results

Of the 52 birds examined, 40 were classified as

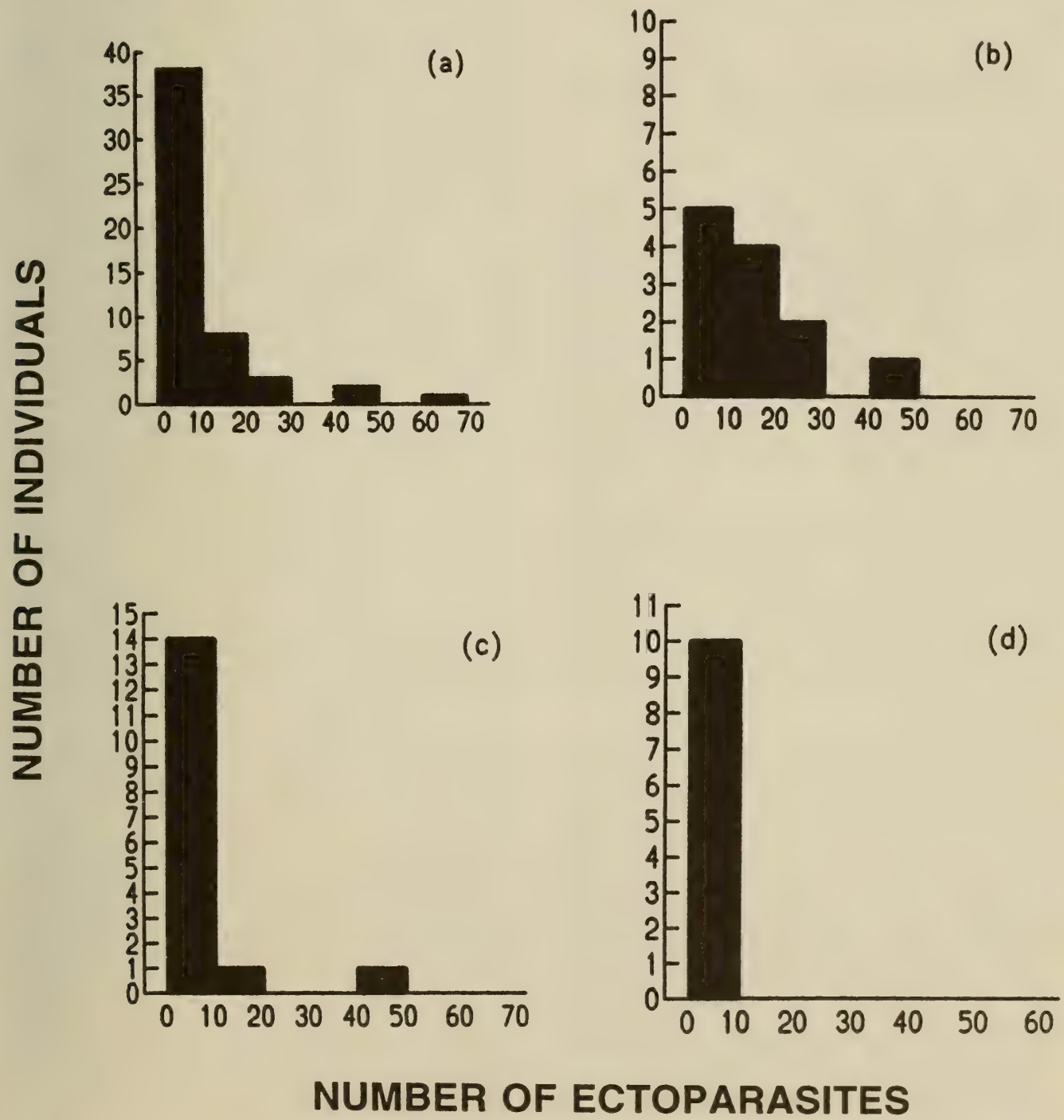

FIGURE 1. Frequency distributions of ectoparasites on lekking Sharp-tailed Grouse: a (all six leks combined), b (lek 2), c (lek 5), and d (lek 6).

TABLE 1. A comparison of ectoparasite number per individual male Sharp-tailed Grouse and its territorial location, peripheral or central on leks, using Mann-Whitney U tests.

	N	Ectoparasites per Individual $\bar{x} \pm SD$	Z^a
All leks			
Peripheral males	26	6±8	-2.37*
Central males	26	13±14	
Lek 2			
Peripheral males	7	13±14	-1.07ns
Central males	5	18±8	
Lek 5			
Peripheral males	8	4±3	-2.11*
Central males	8	12±13	
Lek 6			
Peripheral males	4	5±2	-0.54ns
Central males	6	4±2	

[a]Significance of Z: ns, $P > .28$; *, $P < 0.05$

adults and 12 as yearlings. Males scored as occupying central territories, 50% (N = 26) of all individuals, included only adult birds. The peripheral males, however, consisted of 46.2% (N = 14) adults with the remainder being yearlings.

Only two copulations were recorded during this study, both by central males. One of those males was infested with nine ectoparasites and the other had five. Neither individual had the least or greatest number of ectoparasites in their respective leks; both had infestations within the range found for other birds at the same lek.

None of the sampled males had more than minimal feather damage, even the most heavily infested individuals. No evidence of hematomas were found on any specimens examined. All lekking individuals were classified as being in good condition. Spearman rank correlation analysis showed no significant relationship between ectoparasite number and body mass ($r_s = 0.04$, P = 0.76).

Although the tick *Haemaphysalis* spp. (Baumgartner 1939; Peterle 1954) and the louse *Goniodes* spp. (Snyder 1935; Emerson 1951) have been reported to infest Sharp-tailed Grouse, only the latter was found on the specimens examined. The frequency distribution for data from all the leks (Figure 1a), illustrates the characteristic "hollow" curve type in which most hosts have few parasites and most parasites are on only a few hosts (Eveleigh and Threlfall 1976). Frequency distributions for lek 2 and 5 (Figure 1b,c) also showed the hollow curve type whereas data from lek 6 (Figure 1d) revealed low rates of infestation for all individuals sampled.

Mann-Whitney U tests showed that individuals possessing central territories had significantly more ectoparasites than males occupying peripheral territories in lek 5 and in all leks combined (Table 1). On leks 2 and 6, there was no significant difference in ectoparasitic burden between central and peripheral males (Table 1). Ectoparasite number did not differ significantly (P = 0.49) between adult and yearlings males for all leks combined (adults: N = 40, $\bar{x}$ = 10.65, SD = 13.25; yearlings: N = 12, $\bar{x}$ = 5.92, SD = 4.66). Also, it is noteworthy that peripheral males (independent of age) harboured fewer parasites than central males.

Discussion

In the present study, it was found that during the mating season, there appeared to be neither enough variation in ectoparasites per male in the lekking population, and more importantly, between individuals within a lek to benefit a discriminating female. If females can randomly choose, on average, a mate with few ectoparasites, female choice against ectoparasite-infested males is of no real benefit (Reynolds and Gross 1990). In other studies of lekking bird species, individual ectoparasitic burdens were also found to be low (e.g., Snyder 1935; Peterle 1954; Andersson 1992). Studies which have shown a mating advantage for non-infested males (e.g., Borgia and Collis 1989) were limited methodologically because birds were not sacrificed for a subsequent feather-by-feather examination, and there is a 10% probability that individuals scored as uninfested were really infested (Ash 1960). In other words, it is difficult, to quantify ectoparasite loads without sacrificing the birds, which is not always possible.

No traits, related to ectoparasite loads, which could be used by discriminating females, were found in this study. Feather damage was minimal. Moreover, feather damage would not be a good trait for assessing ectoparasite burden because only basal and medial regions are consumed by lice; thus, feather damage is not readily visible (Clayton 1990). Only in the most severe cases do ectoparasites tatter plumage to the extent that water repellency and insulation are affected (Soulsby 1982).

No cervical lesions were found in this study, although in Sage Grouse (*Centrocercus urophasianus*) lice have been associated with hematomas (e. g., Johnson and Boyce 1989) and mating success (Spurrier et al. 1989). However, in other studies of lekking grouse, ectoparasitic lesions have been reported as rare (e.g., Peterle 1954; Gibson et al. 1991).

Lekking individuals in this study were all in good condition which is not surprising as good health is necessary in establishing and maintaining territories on the lek (Kermott 1982). Ectoparasitic load was not significantly related to body weight although such relationships have been reported in other studies (Snyder 1935; Eveleigh and Threlfall 1976).

Cues consistently correlated with ectoparasite numbers were not evident in the present study. Although occupancy of central territories in Sharp-

tailed Grouse leks has often correlated with male mating success (e.g., Lumsden 1965; Kermott 1982), in the present study, pooled data revealed that central males had significantly larger ectoparasitic burdens compared to peripheral individuals. Within individual leks, only lek 5 showed a similar trend, with lek 2 and 6 showing no significant differences. Perhaps, the relatively large number of individuals examined from lek 5 had a disproportionate influence on the Mann-Whitney U test, when all leks were combined. Nevertheless, central males may sometimes show higher parasitic burdens compared to peripheral individuals due to increased physical contact during the breeding season, as a consequence of small territory sizes (Lumsden 1965) increasing the chance of infestation (Ash 1960). Also, Borgia and Collis (1990) suggested that age-related grooming may be important in controlling louse populations in birds, decreasing loads being associated with increasing age. This was not true with the sharptails studied here as there was no significant difference between ectoparasitic burdens on adult and yearling lekking males.

In overview, it does not appear that the benefit of reduced risk of ectoparasite transmission to female sharptails during mating is a significant factor in mate choice. However, females nonetheless should keep ectoparasites in check because parents can transfer lice to offspring and offspring may be more sensitive to ectoparasites than adults (Marshall 1981; Clayton 1990). This may be the reason why female grouse of lekking species shake vigorously and preen themselves after successful copulation (e.g., Lumsden 1965), as it is known that lice can be transferred during copulation (Eveleigh and Threlfall 1976; Clayton 1990).

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Vascular Plants of a Successional Alvar Burn 100 Days After a Severe Fire and Their Mechanisms of Re-establishment

Paul M. Catling[1,2], Adrianne Sinclair[1], and Don Cuddy[3]

[1] Biology Department, University of Ottawa, 30 Marie Curie Street, P.O. Box 450, Station A, Ottawa, Ontario K1N 6N5 Canada
[2] Agriculture and Agri-food Canada, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada
[3] Ontario Ministry of Natural Resources, Concession Road, Postal Bag 2002, Kemptville, Ontario K0G 1J0 Canada

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In order to describe the vascular plant community 100 days after a severe fire in alvar woodland near Ottawa, Ontario, we set out fifty one m square quadrats at 5 m intervals along transects at each of five sites and recorded presence and cover of vascular plant species in each quadrat. The woodlands that burned were dominated by *Thuja occidentalis*, *Populus tremuloides*, *Abies balsamea*, *Picea glauca*, and *Pinus strobus* in approximate order of importance. The post-fire flora was diverse and mostly native. Although substantial variation occurred in presence, frequency and cover of species between the sites, there was remarkable similarity in a distinctive group of dominants including *Populus tremuloides*, *Geranium bicknellii*, and *Corydalis aurea.* Rare species present in the burned woodland included *Astragalus neglectus*, *Calystegia spithamaea*, *Carex richardsonii*, *Corydalis aurea*, *Muhlenbergia glomerata*, *Panicum flexile, Panicum philadelphicum, Petasites frigidus*, *Scutellaria parvula*, and *Viola nephrophylla*. Of these, *Corydalis aurea* and *Calystegia spithamaea* were frequent. The development of vascular flora following the fire was a consequence of growth from roots, rhizomes, and root crowns that survived the fire, and seeds buried in the soil. Although abundant in the burned woodland, *Corydalis aurea* and *Dracocephalum parviflorum* had not been previously recorded at the site, suggesting that these species are adapted to early post-fire succession, surviving periods of up to 130 years between fires as seeds in a very large and widespread subterranean seed bank. Not only is post-fire succession well underway within a hundred days of a fire, but even in its earliest stages, it appears to serve as a specific niche for a distinctive group of species including some that are rare and restricted. A diverse native flora is involved indicating the importance of management involving removal of woody biomass.

Key Words: alvar, fire, flora, species diversity, rare species, succession, management, biomass removal, prescribed burn, Great Lakes, Ontario, Canada.

Periodically burned woodlands associated with alvar landscapes (i.e., landscapes with more or less drought-maintained open areas on thin soil over essentially flat limestone, dolostone or marble) have recently been recognized as an important part of the alvar ecosystem with regard to protection of rare species and biodiversity and have been termed "successional alvar burns" (Catling and Brownell 1998). Although their importance is generally accepted, the information upon which it is based is limited to common sense, anecdotes, and a single evaluation including data analysis (Catling and Brownell 1998).

On 23 June 1999, 152 hectares of mostly forested terrain in the Burnt Lands near Almonte (Figure 1) was burned. This was a major fire. A shower of ash rained down on streets in downtown Ottawa 40 km away and the fire moved at a rate of 15 m/min. The flames reached well over 30 m into the air and an area at least 1 km in length was severely burned. This area was last burned in 1870. Dry conditions in the relatively shallow soil over porous limestone rock led to a relatively slow return to a mixed boreal and fire prone forest type following the 1870 fire, and it seems likely that fire and post-fire succession has been going on in the area for many hundreds (or thousands) of years.

Brunton (1986*) suggested that the Burnt Lands was a "fire-dependent environment of great provincial significance" that "will require continued renewal by periodic burning if its important natural values are to be preserved." The recent (1999) fire in the Burnt Lands provided an opportunity to gather information related to this suggestion. There are conflicting views about fire in alvar woodland that range from the creation of a long lasting desert to almost immediate return to the pre-fire floristic composition. We agree fully with Brunton's suggestion and further suggest that successional changes occur over decades providing high floristic and faunistic biodiversity as well as spatial-temporal habitat for rare and restricted species. Information on the specific effects of fire is currently insufficient to allow informed choices between management options. The nature of succession in successional alvar burns is not documented with respect to timing of changes or floristic composition, and thus the importance of the succession to biodiversity protection is poorly understood. The compositional changes also relate to the required frequency of implementation of management actions. Finally, biomass removal by fire management is potentially important, not just to the management of biodiversity, but also to the protection of

people and property (from catastrophic fire) where fire-prone vegetation exists in semi-urban areas.

The present study was designed to document the earliest stages of succession thereby providing an indication of its rapidity and potential biodiversity significance including a consideration of whether or not there are species which are adapted to the very earliest stages of the succession. This information is needed for the protection and management of alvars, which are a globally imperilled ecosystem (Brownell 2000) confined in North America to a restricted portion of the Great Lakes region (Catling and Brownell 1995, 1999). Specifically, it is required for the management of the Burnt Lands alvar landscape which has been designated as a provincially significant life science Area of Natural and Scientific Interest (ANSI), with intent to increase protection through designation of provincial crown lands and former federal properties as a provincial nature reserve (Brownell 2000). This requires increasingly comprehensive management and monitoring of significant natural resources.

Methods

Fifty-one m^2 quadrats at 5 m intervals along transects were set out in alvar woodland at each of five sites. The only criteria for determining placement of transect lines was complete burning of all vegetation, separation from each other by more than 300 m, and adequate representation of the burned area through coverage of the eastern, western, northern, southern and central portions. These regions were characterized by different pre-fire tree composition as described below. For each quadrat the total cover (dm^2 estimated as the upper leaf surface area) of each plant species was recorded. Using an estimate of the photosynthetic surface area of the plants rather than the surface area of the quadrat covered by that species permits a more direct correlation between cover values and biomass. The total cover and total frequency for each species at each site was calculated and total overall cover and total overall frequency were tabulated (Table 1). To determine the composition of the original woodland, the tree in each of four quadrants closest to the quadrat centre was identified and measured (dbh-diameter at breast height). The data were then tabulated by species frequency and range of dbh for each site (Table 2). Field work was done on 1–7 October 1999, approximately 100 days after the fire and prior to the first severe frosts. There was no perceptible loss of post-fire vegetation due to dieback in the burned areas sampled.

Status information on the species recorded is provided on a spatial scale of rarity (N,P,R,S,O, see Table 1) with N = nationally rare (Brownell and Larson 1995*); P = provincially rare (Brownell and Larson 1995*); R = regionally rare (eastern Ontario in Brownell and Larson 1995*); S = rare in the St. Lawrence-Ottawa physiographic region (i.e., MNR 6–11 and 6–12, Brownell and Larson 1995*); and O = rare in Ottawa-Carleton (Brunton 1997*). Species listed were also distinguished as native or introduced.

To determine the methods of colonization, plants were excavated and examined 50 days after the fire at site 1 and 100 days after the fire at all sites. Although not quantitative, the observations are considered reliable and useful, and included here since they provide the only source of information on this aspect that is available. Voucher specimens for species recorded were deposited in the vascular plant herbarium of Agriculture and Agri-food Canada (DAO) in Ottawa.

Results and Discussion

General observations

The woodlands that burned were dominated by *Thuja occidentalis*, *Populus tremuloides*, *Abies balsamea*, *Picea glauca*, and *Pinus strobus* in approximate order of importance (Table 2). Similar woodlands are present on alvar landscapes elsewhere in Ontario but often also have Bur Oak (*Quercus macrocarpa* Michx.), and those on the Napanee Plain also have Eastern Red Cedar (*Juniperus virginiana* L.), and those on the Bruce Peninsula and Manitoulin Island also have Jack Pine (*Pinus banksiana* Lamb.) and Red Oak (*Quercus rubra* L.).

Despite variation between sites there was remarkable similarity with respect to a distinctive group of dominants (Table 1). Approximately 100 species were recorded in the quadrats and only 16 of these were introduced. Of the total species, 19 exceeded 5% overall frequency with only 3 of the 19 being introductions. The majority of the plants and over 90% of the cover at each site was comprised of native species. Thus the flora developing after the fire was comprised largely of native species and it was relatively diverse (Table 1).

Variation between sites

The species which re-colonize a burn and the means of colonization can be expected to vary depending upon the intensity of the fire. There is natural variation in the amount of heat generated, and fire-fighting efforts (such as water bombing) undoubtedly will locally reduce the penetration of heat into the soil. This may add to the fine scale variation in patterns of re-colonization but is unlikely to alter the range of means observed over 50 quadrats. Consequently variation in post-fire colonization between sites is most likely to be related to factors other than fire intensity.

Surface coverage of plants varied from approximately 10–50% among the five sites and species with cover values exceeding 1% of quadrat surface varied from three to eight in number at a site. The

*See Documents Cited section.

TABLE 1. Total cover (dm^2) in 50 quadrats, percentage frequency, and status (N = nationally rare (Brownell 1995); P = provincially rare (Brownell 1995); R = regionally rare (eastern Ontario in Brownell 1995); S = rare in the St. Lawrence-Ottawa physiographic region (i.e., MNR 6–11 and 6–12, Brownell 1995); O = rare in Ottawa-Carleton (Brunton 1997)) for vascular plant species in the herb layer (less than 1 m above ground) in five burned woodlands approximately 100 days after a fire in the Burnt Lands near Almonte, Ontario. The data are based on 50 one m^2 quadrats at each site laid out along transects within an area of approximately 1 hectare. Species are listed in descending order of overall cover. Species marked with an asterisk (*) are introduced. Note that *Pinus banksiana* is a native species that is believed to be introduced at this site based on absence of older trees in surrounding forests and past plantings.

Scientific Name	Total Cover (dm^2) 1	2	3	4	5	Total Overall	% Frequency 1	2	3	4	5	Mean Overall
Populus tremuloides Michx., Trembling Aspen	329.4	417.3	1296.6	255.9	64.4	2363.6	74	86	96	64	42	72.4
Geranium bicknellii Britton, Bicknell's Crane's-bill	18.9	297.6	572	198.9	240.8	1328.2	26	78	94	80	74	70.4
Pteridium aquilinum (L.) Kuhn var. *latiusculum* (Desv.) L. Underw. ex A. Heller, Eastern Bracken-fern	–	156.1	247	–	–	403.1	–	38	28	–	–	13.2
Corydalis aurea Willd. ssp. *aurea*, Golden Corydalis (**SO**)	83.1	15.9	88.2	48.8	26.9	262.9	66	14	32	30	26	33.6
Aster macrophyllus L., Large-leaved Aster	32.2	61.9	46.8	–	–	140.9	14	32	8	–	–	10.8
Medicago lupulina L., Black Medick (*)	2.5	2.5	58	0.4	–	63.4	4	2	28	2	–	7.2
Rosa acicularis Lindl. ssp. *sayi* (Schwein.) W. Lewis, Prickly Rose	–	–	55.6	6.4	0.2	62.2	–	–	46	12	2	12.0
Symphoricarpos albus (L.) S. F. Blake, Snowberry	22.4	17.9	19.5	–	0.5	60.3	24	36	20	–	2	16.4
Apocynum cannabinum L., Indian Hemp	28	13.2	8	–	–	49.2	4	12	8	–	–	4.8
Dracocephalum parviflorum Nutt., Small-flowered Dragonhead	–	33.2	–	2.3	10.7	46.2	–	28	–	2	14	8.8
Populus balsamifera L. ssp. *balsamifera*, Balsam Poplar	–	–	29.8	0.7	–	30.5	–	–	12	2	–	2.8
Rhus rydbergii Small ex Rydb., Poison-ivy	9.5	–	14.8	1.8	0.4	26.5	26	–	30	10	2	13.6
Petasites frigidus (L.) Fr., Sweet-coltsfoot (**S**)	–	–	15.8	9.3	–	25.1	–	–	6	8	–	2.8
Aralia nudicaulis L., Wild Sarsaparilla	–	11.1	13	–	–	24.1	–	14	18	–	–	9.2
Aster ciliolatus Lindl., Ciliolate Aster	3	–	1.6	11.2	7.8	23.6	2	–	6	10	10	5.6
Taraxacum officinale G. Weber, Common Dandelion (*)	13.2	1.8	2.8	3.0	–	20.8	16	4	6	6	–	6.4
Senecia pauperculus Michx., Balsam Groundsel	–	–	–	1.2	19.6	20.8	–	–	–	4	7	2.2
Cirsium vulgare (Savi) Ten., Bull Thistle (*)	–	–	–	7	11	18.0	–	–	–	4	4	1.6
Hieracium piloselloides Vill., Glaucous King Devil (*)	1	2	6	1.8	4.4	15.2	2	2	8	6	14	6.4
Campanula rotundifolia L., Harebell	1.5	–	3.7	3.0	6.7	14.9	6	–	10	12	16	8.8
Aquilegia canadensis L., Wild Columbine	4	–	3.3	0.1	6.6	14.0	4	–	4	2	12	4.4
Verbascum thapsus L., Common Mullein (*)	1.5	–	11.9	–	2	15.4	2	–	12	–	2	3.2
Waldsteinia fragarioides (Michx.) Tratt., Barren Strawberry	2	4	3.4	–	2.5	11.9	8	6	10	–	14	7.6
Chenopodium simplex (Torr.) Raf., Maple-leaved Goosefoot	1	–	9	1.3	–	11.3	2	–	6	2	–	2.0
Rubus pubescens Raf., Dwarf Raspberry	–	–	–	8.4	–	8.4	–	–	–	18	–	3.6
Celastrus scandens L., Climbing Bittersweet	–	–	8	–	–	8.0	–	–	6	–	–	1.2
Hypericum sp., St. John's-wort	–	8	–	–	–	8.0	–	2	–	–	–	0.4
Rubus cf. *pubescens* Raf., Dwarf Raspberry	–	–	8	–	–	8.0	–	–	16	–	–	3.2
Rhus typhina L., Staghorn Sumac	7.2	–	–	–	–	7.2	18	–	–	–	–	3.6
cf. *Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult., Poverty Oat Grass	–	–	7	0.7	–	7.7	–	–	2	6	–	1.6

continued

TABLE 1. *continued*

Scientific Name	Total Cover (dm²) 1	2	3	4	5	Total Overall	% Frequency 1	2	3	4	5	Mean Overall
Lonicera sp., Honeysuckle	–	–	7	–	–	7.0	–	–	2	–	–	0.4
Aquilegea canadensis L., Wild Columbine	–	–	–	–	6.6	6.6	–	–	–	–	12	2.4
Prunus cf. *virginiana* L. ssp. *virginiana*, Choke Cherry	–	–	6	–	0.2	6.2	–	–	2	–	2	0.8
Panicum acuminatum Sw. var. *acuminatum*, Acuminate Panic Grass	1.7	–	2	0.2	3.7	7.6	10	–	4	4	10	5.6
Viola adunca Sm., Hooked-spur Violet	2.7	–	3.1	–	–	5.8	10	–	22	–	–	6.4
Solidago nemoralis Aiton, Gray-stemmed Goldenrod	–	–	5	–	0.7	5.7	–	–	4	–	8	2.4
Rubus cf. *idaeus* L. ssp. *melanolasius* (Dieck) Focke, Wild Red Raspberry	–	–	4	–	2	6.0	–	–	2	–	2	0.8
Cirsium sp., thistle	1.5	2	2	1.4	–	6.9	2	2	4	6	–	2.8
Rosa sp., rose	2	3.5	–	–	–	5.5	2	10	–	–	–	2.4
Clinopodium vulgare L., Wild Basil	–	–	5	–	–	5.0	–	–	2	–	–	0.4
Vicia sp., Vetch (*)	5	–	–	–	–	5.0	2	–	–	–	–	0.4
Trichostema brachiatum L., False Pennyroyal	–	–	–	–	5	5.0	–	–	–	–	2	0.4
Viburnum rafinesquianum Schult., Downy Arrow-wood	–	–	5	–	–	5.0	–	–	2	–	–	0.4
Carex sp., sedge	–	1	3	0.4	–	4.4	–	2	24	8	–	6.8
Panicum linearifolium Nash, Narrow-leaved Panic Grass	–	–	1.3	–	3	4.3	–	–	6	–	2	1.6
Vicia cracca L., Tufted Vetch (*)	–	–	3.4	0.5	0.1	4.0	–	–	8	2	2	2.4
Maianthemum canadense Desf., Wild Lily-of-the-valley	2	–	1.5	0.3	0.1	3.9	4	–	20	4	2	6.0
cf. *Lilium philadelphicum* L., Wood Lily	–	–	3	–	0.2	3.2	–	–	6	–	4	2.0
Prunus cf. *pensylvanica* L., f. Pin Cherry	–	–	3.1	–	–	3.1	–	–	12	–	–	2.4
Calystegia spithamaea (L.) Pursh ssp. *spithamaea*, Low Bindweed **(RSO)**	3.1	–	–	–	–	3.1	–	26	–	–	–	5.2
Cornus stolonifera Michx., Red-osier Dogwood	–	–	3	–	–	3.0	–	–	8	–	–	1.6
Astragalus neglectus (Torr. & A. Gray) E. Sheld., Neglected Milkvetch **(PRSO)**	–	–	3	–	–	3.0	–	–	2	–	–	0.4
Panicum philadelphicum Bernh. ex Trin., Wood Panic Grass **(S)**	–	–	3	–	–	3.0	–	–	2	–	–	0.4
Carex cf. *intumescens* Rudge, Bladder Sedge	–	–	3	–	–	3.0	–	–	2	–	–	0.4
Amelanchier alnifolia (Nutt.) Nutt. ex R. Roem ssp. *compacta* (Nielsen) McKay, Juneberry	–	2	2.3	0.6	–	4.9	–	2	6	2	–	2.0
Solidago juncea Aiton, Early Goldenrod	–	–	–	–	2.3	2.3	–	–	–	–	4	0.8
Solidago hispida Muhl. var. *hispida*, Hairy Goldenrod	–	–	1.3	–	2.2	3.5	–	–	2	–	6	1.6
Solidago ptarmicoides (Nees) B. Boivin, Upland White Goldenrod **(S)**	–	–	–	–	2.1	2.1	–	–	–	–	6	1.2
unidentified rosette 2	–	–	2	–	–	2.0	–	–	2	–	–	0.4
Cornus canadensis L., Bunchberry	–	–	2	–	–	2.0	–	–	2	–	–	0.4
Antennaria sp., Pussytoes	2	–	–	–	–	2.0	–	2	–	–	–	0.4
Fragaria virginiana Miller ssp. *virginiana*, Scarlet Strawberry	–	–	–	1.0	0.9	1.9	–	–	–	2	4	1.2
Carex richardsonii R. Br., Richardson's Sedge **(SO)**	–	–	–	0.6	1.2	1.8	–	–	–	10	10	4.0

continued

TABLE 1. *continued*

Scientific Name	Total Cover (dm^2) 1	2	3	4	5	Total Overall	% Frequency 1	2	3	4	5	Mean Overall
Panicum flexile (Gattinger) Scribn., Wiry Panic Grass **(S)**	–	–	–	–	1.8	1.8	–	–	–	–	8	1.6
Solidago sp., goldenrod	1.5	–	–	–	–	1.5	2	–	–	–	–	0.4
Rosa blanda Aiton, Smooth Rose	–	–	–	1.1	0.3	1.4	–	–	–	6	2	1.6
Trifolium sp., Clover (*)	–	–	1.2	–	0.1	1.3	–	–	6	–	2	1.6
Sanicula sp., snakeroot	–	–	1.3	–	–	1.3	–	–	4	–	–	0.8
Agrostis hyemalis (Walter) B.S.P., Colonial Bent Grass	–	–	–	0.7	0.6	1.3	–	–	–	2	4	1.2
Carex pellita Willd., Woolly Sedge	–	–	–	0.7	0.5	1.2	–	–	–	6	4	2.0
Spiraea alba Du Roi, Narrow-leaved Meadow-sweet	–	–	1.2	–	–	1.2	–	–	2	–	–	0.4
Rhamnus frangula L., Glossy Buckthorn (*)	–	–	–	1.2	–	1.2	–	–	–	2	–	0.4
Danthonia spicata (L., P. Beauv. ex Roem. & Schult., Poverty Oat Grass	–	–	–	1.0	1.0	2.0	–	–	–	8	1.6	1.9
Diervilla lonicera Miller, Bush Honeysuckle	–	–	1	–	–	1.0	–	–	2	–	–	0.4
Viola cf. *renifolia* A. Gray, Kidney-leaved Violet	–	–	1.0	–	–	1.0	–	–	2	–	–	0.4
Trifolium cf. *repens* L., White Clover (*)	–	–	1	–	–	1.0	–	–	2	–	–	0.4
Equisetum scirpoides Michx., Dwarf Scouring-rush	–	–	1	–	–	1.0	–	–	2	–	–	0.4
unidentified rosette 1	–	–	1	–	–	1.0	–	–	2	–	–	0.4
Chaenorrhinum minus (L.) Lange Dwarf Snapdragon (*)	–	–	–	–	0.8	0.8	–	–	–	–	6	1.2
unidentified rosette 3	–	–	–	0.7	–	0.7	–	–	–	6	–	1.2
grass	–	–	–	–	0.7	0.7	–	–	–	–	4	0.8
Viola nephrophylla Greene, Northern Bog Violet **(RS)**	–	–	–	–	0.6	0.6	–	–	–	–	4	0.8
Arctostaphylos uva-ursi (L.) Spreng., Common Bearberry	–	–	–	–	0.6	0.6	–	–	–	–	4	0.8
Houstonia sp.	–	–	–	0.5	–	0.5	–	–	–	2	–	0.4
Muhlenbergia glomerata (Willd.) Trin., Glomerate Satin Grass **(S)**	–	–	–	–	0.5	0.5	–	–	–	–	2	0.4
Carex castanea Wahlenb., Chestnut Sedge	–	–	–	0.5	–	0.5	–	–	–	2	–	0.4
Hypericum perforatum L., Common St. John's-wort (*)	–	–	–	–	0.5	0.5	–	–	–	–	4	0.8
unidentified rosette 4	–	–	–	–	0.4	0.4	–	–	–	–	2	0.4
Glyceria sp., Manna Grass	–	–	–	0.3	–	0.3	–	–	–	2	–	0.4
Pinus banksiana Lamb., Jack Pine (*)	–	–	–	–	0.3	0.3	–	–	–	–	4	0.8
Carex sect. *Ovales*	–	–	–	0.3	–	0.3	–	–	–	2	–	0.4
unidentified shrub	–	–	–	–	0.2	0.2	–	–	–	–	2	0.4
Plantanthera sp., orchid	–	–	–	0.2	–	0.2	–	–	–	4	–	0.8
Panicum sp.	–	–	–	–	0.1	0.1	–	–	–	–	2	0.4
Prunella vulgaris L. ssp. *vulgaris,* Common Heal–all (*)	–	–	–	0.1	–	0.1	–	–	–	2	–	0.4
Scutellaria parvula Michx., Small Skullcap **(S)**	–	–	–	0.1	0.1	0.2	–	–	–	2	6.4	1.7
cf. *Rhamnus cathartica* L., Common Buckthorn (*)	–	–	–	0.1	–	0.1	–	–	–	2	–	0.4

total species recorded in quadrats at a site varied from approximately 18 to approximately 50 (Table 1). These data are approximate because only portions of sites were sampled, some small immature plants could not be identified accurately, and some species noted at sites were not recorded within quadrats.

Site 1, previously dominated by White Spruce and Trembling Aspen (Table 2) had a relatively low diversity of 25 species. This site had the lowest cover of *Geranium bicknellii,* a relatively high cover of *Corydalis aurea* and the highest cover values for *Apocynum cannabinum* and *Symphoricarpos alba* (Table 1).

Site 2 was previously dominated by Trembling Aspen and Eastern White Cedar (Table 2). *Aster macrophyllus* and *Dracocephalum parviflorum* reached their highest cover values here. *Corydalis aurea* had its lowest cover value at this site. Diversity was lowest at this site with 18 species recorded in quadrats (Table 3).

Site 3, previously dominated by Eastern White Cedar and Balsam Fir (Table 2), had a relatively high diversity of approximately 50 species. This site had the highest cover of Trembling Aspen regrowth, the highest cover of *Geranium bicknellii* and *Corydalis aurea*, highest cover of many other species such as *Rosa acicularis*, *Chenopodium simplex* and *Petasites frigidus*. This site also had a relatively high cover value for some weeds such as *Medicago lupulina* and *Verbascum thapsus* (Table 1).

Eastern White Cedar had previously dominated site 4 (Table 2). Approximately 40 species were recorded here. This site had the highest cover values for *Aster ciliolatus* and *Rubus pubescens*. *Aster macrophyllus* and *Symphoricarpos albus* were conspicuously absent.

Site 5 had been a wooded edge of an alvar opening that was dominated by Eastern White Cedar and White Spruce. Not surprisingly, being a wooded edge, it was the only site, or the site with largest cover values, for a number of species characteristic of alvar openings such as *Aquilegia canadensis, Carex richardsonii, Panicum flexile, Senecio pauperculus*, *Solidago juncea,* and *Trichostema brachiatum.*

Dominant species

The species accounting for the highest frequency and cover 100 days after the fire were *Populus tremuloides, Geranium bicknellii* and *Corydalis aurea* (Table 1). These three were present at all of the five burned woodland sites, and their frequency values ranged from 33.6 to 72.4% of the total 250 quadrats. Each of these species had cover values exceeding 1%. Other species were much less important in terms of cover (Table 1), or in the cases of *Aster macrophyllus* and *Pteridium aquilinum*, were not present at all sites and had a much lower mean frequency (Figure 1).

Significant Species

The rare species recorded in quadrats at the five sites included *Astragalus neglectus*, *Calystegia spithamaea*, *Carex richardsonii*, *Corydalis aurea*, *Muhlenbergia glomerata*, *Panicum flexile, Panicum philadelphicum, Petasites frigidus*, *Scutellaria parvula*, and *Viola nephrophylla*. Only the first mentioned is provincially rare, the others being rare regionally (Table 1 and methods). Most of these rare species were infrequent, but *Corydalis aurea* had a relatively high overall frequency (33.3 %) and a relatively high overall cover (Table 1). *Calystegia spithamaea* was also frequent with 5.25 % frequency overall but 26 % frequency at one site. The early post-fire flora thus includes 10 rare species of which two are relatively frequent, one of them being a dominant.

Not only was the regionally rare *Corydalis aurea* a dominant of the recently burned woodland, it was not recorded in a relatively comprehensive checklist of the Burnt Lands area (Brunton 1986*), nor was it listed by White (1979) in an enumeration of the rare species of the site. It is a rather uncommon and puzzling native species often associated with disturbed ground, such as bulldozed tracks though dry calcareous woodland, where it occurs with introduced weeds. *Corydalis aurea* is evidently a species of successional alvar burns that becomes abundant due to release from the seedbank in the early post-fire succession, only to disappear again in the later stages of succession explaining why earlier botanists documenting the flora did not find it. They needed a fire

TABLE 2. Tree frequencies and dbh range (cm) of fire–killed trees in four quadrants of each of 50 points laid out along transects within an area of approximately 2 acres in each of four burned woodlands approximately 100 days after a severe fire in the Burnt Lands near Almonte, Ontario.

Species	% Frequency/DBH range			
	1	2	3	4
Picea glauca (Moench) Voss, White Spruce	17/8–36	1.5/15–20	11.5/6–23	1.5/16–17
Pinus strobus L., Eastern White Pine	3.5/9–28	1.5/6–23	2.5/30–40	2.5/14–32
Populus tremuloides Michx., Trembling Aspen	20.5/5–23	14/9–25	9/7–28	4/11–26
Thuja occidentalis L., Eastern White Cedar	5.5/7–21	21.5/5–31	17.5/5–32	55/5–25
Abies balsamea (L.) Miller, Balsam Fir	4.5/6–20	5.5/6–18	20/5–18	6.5/5–14
Betula papyrifera Marshall, White Birch	–	–	0.5/17	–

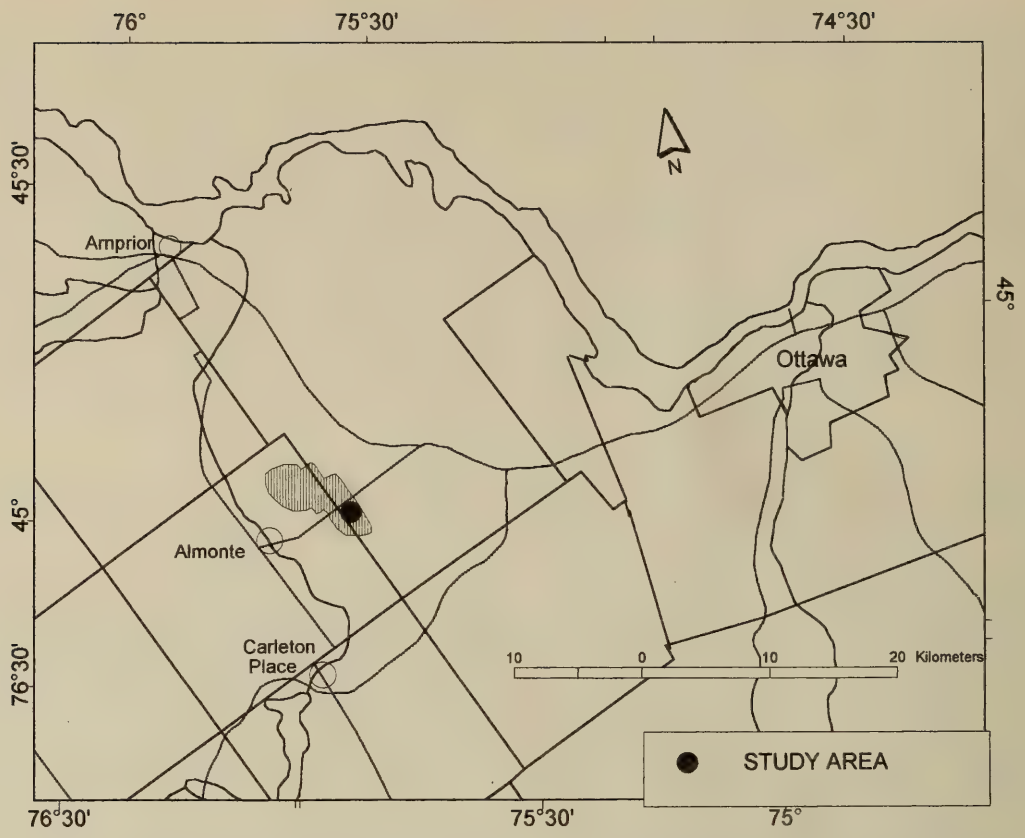

FIGURE 1. Ottawa region of eastern Ontario showing the location of the Burnt Lands (shaded) and the study area (dot).

to see it and there had not been one for more than a hundred years.

Another particularly interesting case is that of *Dracocephalum parviflorum* which was also not listed by Brunton (1986*). It appears to be very similar to *Corydalis aurea* in its natural habitat and niche. Although not found previously in the area it had a frequency of 28% at site 2 and an overall frequency of 8.8%, and it also had the 10th highest cover value of all species.

Although we have highlighted the abundant rare species in the early post-fire succession, it is to be noted that species may be rare in a particular successional stage, but may also be largely or entirely dependent on that stage, and even characteristic of it. This may be true for *Chenopodium simplex* and *Astragalus neglectus*. The quadrats under-represent significance since the sampled ground is so small that population size is not adequately accounted for. At least 100 plants of *Astragalus neglectus* were seen in the burned woodland but frequency and cover was so low as to prevent this species from being well represented in the quadrat sample of 250 m^2. Although present, *Cirsium discolor* was not represented in any of the quadrats, and it was possibly too late in the season to discern *Cypripedium arietinum*. The quadrat sample, although ensuring an accurate and quantitative assessment provides only a minimal picture of early post-fire diversity and significant flora.

Means of colonization

The development of vascular flora following the fire was a consequence of growth from: (1) roots as in the case of the root suckers of *Populus tremuloides* and *Populus balsamifera*; (2) rhizomes and root crowns as in *Apocynum cannabinum, Aralia nudicaulis, Aster ciliolatus, Aster macrophyllus, Pteridium aquilinum, Petasites frigidus, Symphoricarpos albus*; and (3) an ancient soil seed bank as in *Corydalis aurea, Dracocephalum parviflorum* and *Geranium bicknellii.* In the case of many species, especially those of the woodland edge, such as *Senecio pauperculus* and *Campanula rotundifolia*, the relative contribution of seeds and rhizomes was unclear.

Of the introduced species, *Medicago lupulina* appeared to have developed from seed in the soil whereas *Taraxacum officinale* and *Hieracium piloselloides* appeared to have developed entirely from root crowns and/or rhizomes. Regrowth of *Rhamnus frangula* from roots or root crowns at one site varied from 1–1.5 m after 100 days. There is a potential for this species to have a significant negative influence on native species diversity in the post-fire succession and to present problems in the management involving removal of woody biomass, but there was little evidence of it in the burned woodlands (Table 1).

Species that might have provided seed sources from the current year produced seed too late (e.g.,

FIGURE 2. Alvar woodland previously dominated by White Spruce and Trembling Aspen, 100 days after a severe fire. The herb layer is dominated by *Populus tremuloides, Corydalis aurea*, and *Apocynum cannabinum*. Photo by P. M. Catling.

Apocynum cannabinum), or were insufficiently abundant to allow the level of colonization (e.g., *Corydalis aurea* and *Dracocephalum parviflora* which were not present prior to the fire) or could not provide the cover observed in so short a time (e.g., *Populus tremuloides* with relatively small seeds). The only tree seedlings observed were Jack Pine in the burned woodland edge (Table 1).

With respect to the ancient seed bank, for so many seeds to have survived continuously, avoiding predation, rotting, and drying out over a period of more than a hundred years, there must have been many thousands added to each square metre of the soil early after the last fire. The development of the flora after 100 days, provides strong evidence for such an enormous seed input.

Conclusions

The present observations provide further support for the beneficial effects of fire (with some restrictions: see Catling and Brownell 1998), or other woody biomass removal methods, on alvar landscapes. Not only is post-fire succession well underway within a hundred days of a spring or early summer fire, but even in its earliest stages, it appears to serve as a specific niche for a distinctive group of species including some that are rare and restricted. This phenomenon is not confined to alvar woodland. In a review of the literature relating to post-fire succession and buried seeds, Abrams and Dickman (1984) note that germination of many species is restricted to the first year after a fire. Some of these early post-fire colonizers are absent during the later post-fire succession and in some cases not present during the second year. The fact that the natural recovery of alvar woodland is so rapid and involves a diverse and distinctive group of predominantly native species in the initial stages further suggests the importance of fire as a natural process in alvar woodlands, and its importance as a potentially valuable management option.

As in the alvar woodland studied here, *Geranium bicknellii* dominates the vegetation cover during the first year after a fire in Jack Pine woodlands of northern lower Michigan, but disappears subsequently. The seeds were found to be dependent on heat from the fire for germination and reduced dependence on heat in seed from other regions suggested ecotypic variation in germination behaviour (Abrams and Dickman 1984). It appears that a similar mechanism may operate for other species reported here as dominant early colonizers such as *Corydalis aurea* and *Dracocephalum parviflorum*. Subtle local adaptations to natural processes such as heat from fires suggests that management using the natural processes is most desirable. For example, woody biomass may be removed by cutting but the heat required for germination is then not provided. Since alvar woodlands are naturally prone to fire, the management of woody biomass using prescribed burn is necessary for protection of people and their property (from fire) as well as the protection of significant natural resources.

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New Records of Land Snails from the Mountains of Northwestern British Columbia

ROBERT G. FORSYTH

2574 Graham Street, Victoria, British Columbia V8T 3Y7 Canada; e-mail: robert_forsyth@telus.net

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Terrestrial gastropod faunas of vast areas of northern and central British Columbia are extremely poorly known. I record new distributional records of *Punctum randolphii* (Dall, 1895), *Microphysula cookei* (Pilsbry, 1922), *Pristiloma arcticum* (Lehnert, 1884), *Vertigo columbiana* (Pilsbry & Vanatta, 1900) and other land snails from the Babine and Bulkley Ranges, Nechako Plateau, and Boundary Range of northwestern British Columbia. Records of *Punctum randolphii* and *Vertigo columbiana* are the first higher elevation localities in British Columbia. *Pristiloma arcticum* was collected from one site in the Babine Mountains and is newly recorded from the province. *Microphysula cookei*, previously known only from southern British Columbia and adjacent Washington, occurs north to the Babine and Hazelton Ranges, Nechako Plateau, and Boundary Range. While sharing many species in common, the mountain snail fauna differed from that of the adjacent Bulkley Valley by the inclusion of "coastal" and montane elements. Absent from the drier valley floor, *Punctum randolphii*, *Microphysula cookei, Vertigo columbiana* and *Vespericola columbianus* are considered coastal species whose distributions extend far inland along climatically favourable corridors.

Key Words: terrestrial gastropods, range extensions, new records, *Microphysula cookei*, *Punctum randolphii*, *Pristiloma arcticum*, *Vertigo columbiana*, Babine Range, Bulkley Range, Nechako Plateau, Boundary Range, northwestern British Columbia.

The terrestrial gastropods of northern British Columbia have received little attention, and the fauna of this vast region of the province is virtually unsurveyed. From 1995 to 1999, I made periodic observations of gastropods in the vicinity of the town of Smithers in northwestern British Columbia, on the northwestern edge of the Nechako Plateau, and at approximately 150 localities in the mountains and plateaus of central and northern British Columbia. Collections from the Babine Range (Skeena Mountains) and Bulkley Range (Hazelton Mountains) provided interesting new distribution records of land snails and demonstrated that several of these species, which are predominantly coastal in distribution, occur much further inland in British Columbia than previously thought. Therefore, the purpose of this paper is to document these records from this little-studied region of British Columbia.

Localities

I found terrestrial snails at 13 localities in the Bulkley Range (Hazelton Mountains) and Babine Range (Skeena Mountains), east of the Coast Mountains, near the northwestern edge of the Nechako Plateau (Figure 1). Both mountain ranges are considered part of the Interior System but are contiguous with lee side of the Kitimat Range of the Coast Mountains (Holland 1976). With one exception that is in the Alpine Tundra zone (AT), sites are classified in the Englemann Spruce–Subalpine Fir biogeoclimatic zone (ESSF) of Meidinger and Pojar (1991). Two additional localities (14 and 15 in the Appendix) are not part of the Bulkley–Babine series but are included because they further add distributional data for the species discussed. Exact localities, descriptions of sites, and dates when visited are in the Appendix.

Records

I collected 14 species of terrestrial snails from the Bulkley and Babine Ranges (Table 1). Nine of these species also were found in the Bulkley Valley, which divides these two mountain ranges, or on lower mountain slopes at elevations between ca. 500–900 m (Table 1). However, five species appear restricted to the mountains: *Punctum randolphii*, *Microphysula cookei*, *Vespericola columbianus*, *Pristiloma arcticum*, and *P. chersinella*. Species that also occur in coastal British Columbia include *P. randolphii*, *M. cookei* and *V. columbianus* (Pilsbry 1940, 1946, 1948; Cameron 1986). Accounts of particularly noteworthy records follow.

Voucher specimens of all species reported here are deposited in the Invertebrate Collection, Royal British Columbia Museum, Victoria (Table 2). Additional material is in the personal collection of the author.

Microphysula cookei (Pilsbry, 1922),
Vancouver Snail

M. cookei (Figure 2) was described from specimens from Cameron Lake, Vancouver Island (Pilsbry 1922), and later recorded from Quamisham District near Duncan, British Columbia, and English Camp, San Juan Island, Washington (Pilsbry 1940).

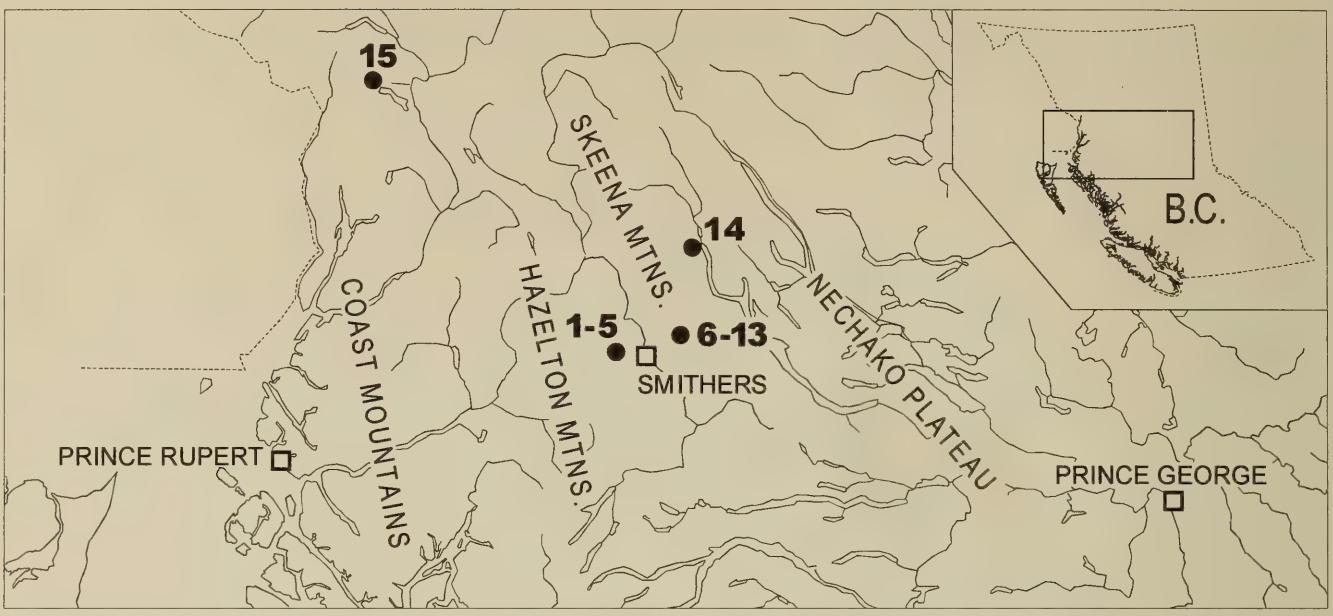

FIGURE 1. Map of study area showing relative distances between localities. Localities 1–5: Hudson Bay Mountain, Bulkley Range (Hazelton Mountains). Localities 6–13: Babine Range (Skeena Mountains). Locality 14: Tsezakwa Creek (Nechako Plateau). Locality 15: Bear River Pass, Boundary Range (Coast Mountains).

Cameron (1986) identified *M. cookei* from four localities; three were in the Chilliwack Valley in southwestern mainland British Columbia, and one was at Buttle Lake on Vancouver Island (ca. 49°41′N, 125°33′W). The Buttle Lake site was the most northern record of this species.

In the vicinity of Smithers, *Microphysula cookei* was found in the Babine Range (sites 6, 7, 8, 9, 10, 11 and 13) and Hazelton Range (sites 3 and 4). Two additional records (sites 14 and 15) extend the range of this species even further north. Site 15, overlooking Strohn Lake, approximately 759 km (on a bearing of 319°) from Buttle Lake, Vancouver Island, is the most northern of these new records and represents a significant range extension.

Microphysula cookei occupies barren rocky sites with minimal vegetation and loose broken rock near the timberline (sites 6, 7 and 8), but also occurs in forested sites (3, 4, 9, 10, 11 and 13). *M. cookei* appears to require moist conditions, as does its congener *M. ingersolli* (Bland, 1875) (Bequaert and Miller 1973), and was not found in the relatively drier, lower elevations within the Bulkley Valley (below 900 m).

Punctum randolphii (Dall, 1895), Conical Spot[1]

Punctum randolphii is a common snail in deciduous and mixed forests of the south coast of British Columbia and is often particularly abundant in association with Bigleaf Maple, *Acer macrophyllum* (personal observation). Its range is generally regarded to be from Vancouver Island to Oregon, east to Idaho (Pilsbry 1948) and south to the Klamath Mountains of northern California (Roth 1985). However, Tuthill (1963) reported "*Punctum* species" (later referred to as *Punctum species* cf. *randolphi* by Tuthill and Johnson [1969]) from the vicinity of the Martin River Glacier, south-central Alaska, and it has also recently been found on the Queen Charlotte Islands (Forsyth, unpublished).

I collected *Punctum randolphii* from leaf litter and other dead plant material at montane sites on both sides of Bulkley Valley at elevations between 900–1200 m (sites 2, 3, 5, 9, 11 and 13). The species was noticeably absent from lower mountain slopes and from the valley. At all sites, herbaceous vegetation and shrubs (including Douglas Maple, *Acer glabrum*, and Red Elderberry, *Sambucus racemosa*) were abundant. Deciduous trees were also present, including Trembling Aspen, *Populus tremuloides*, and willow, *Salix spp.*

The new records of *Punctum randolphii* help fill in a large gap between the isolated Alaska record (Tuthill 1963; Tuthill and Johnson 1969) and the better known southern range of the species. These records are the first from higher elevations in British Columbia and fall within this species' known altitudinal range: sea level to elevations up to 1130 m in Washington (Branson 1980) and to 4500 ft [1372 m] in Idaho (Pilsbry 1948).

[1]As a convention in his *Land Mollusca of North America, North of Mexico* and to avoid "... a needless tax on the memory", Pilsbry used a single *i* for all species names derived from male proper names even when the original spelling was with a double *i* (Pilsbry 1948: XXXIX). I have used here the original (see Dall, 1895) and correct spelling of the species epithet: *randolphii*.

TABLE 1. Species found at collecting sites (numbered 1–13) in the Babine and Bulkley Ranges. The presence of a species in the adjacent Bulkley Valley (500 to less than 900 m) is also indicated.

Species	Localities													
	1	2	3	4	5	6	7	8	9	10	11	12	13	Valley
Columella edentula								+	+				+	+
Discus whitneyi			+	+		+		+	+					+
Euconulus fulvus		+		+		+	+		+	+	+	+	+	+
Microphysula cookei			+	+		+	+	+	+	+	+		+	
Nesovitrea binneyana occidentalis				+	+									+
Pristiloma chersinella						+			+					
Pristiloma arcticum										+				
Punctum randolphii		+	+		+				+		+		+	
Vertigo columbiana					+									
Vertigo modesta forms						+		+		+	+	+	+	+
Vespericola columbianus				+	+									
Vitrina pellucida	+					+					+	+	+	+
Zonitoides arboreus				+										+
Zoogenetes harpa				+										+

Pristiloma arcticum (Lehnert, 1884), Arctic Tightcoil

Pristiloma arcticum arcticum is widely distributed from Point Barrow and Attu Island, Aleutian Islands, Alaska south to Washington, and in Kamchatka, Hokkaido and the Kurile Islands (Pilsbry 1946; Roth and Lindberg 1981). There is also a named subspecies [*P. arcticum crateris* Pilsbry, 1946] from Crater Lake, southern Oregon, but it is rather weakly delineated from the typical subspecies. No prior published records exist for either these taxa from British Columbia. Specimens of *P. arcticum* (*sensu lato*) (Figure 3A) were collected from only one locality, a forested site (10) in the Babine Mountains. Based on Pilsbry's figures (1946: 401, 402, fig. 214, 215) of *P. arcticum arcticum* and *P. a. crateris*, the British Columbia material resembles the latter in the shape of the aperture.

Previously, I located another species of *Pristiloma*, *P. chersinella* (Dall, 1866) (Figure 3B), from nearby sites (6 and 9) in the Babine Mountains (Forsyth 1999*). Both these species appear to be associated with montane habitats, but *P. chersinella* appears to prefer vegetated rockslides, where *P. arcticum* has not yet been found.

Vertigo columbiana (Pilsbry & Vanatta, 1900), Columbia Vertigo, and other *Vertigo* species

Small snails of the genus *Vertigo* were common at many sites in this study (see Table 2). At least two species were found.

At site 5 on Hudson Bay Mountain, two specimens of *Vertigo columbiana* were collected (Figure 4). These shells are identified by their small size (2.0 and 2.1 mm), pale yellowish colour, unthickened apertural lip and relatively smooth shell surface. Additionally, the crest (a ridge on the last whorl behind the apertural lip) is low to moderately developed and there are four apertural "teeth." *Vertigo columbiana* was known from Vancouver Island, British Columbia, to Douglas County, Oregon (Pilsbry, 1948). Additionally, there is a record [first introduced by Dall (1905) and repeated by Pilsbry

*See Documents Cited section.

TABLE 2. Voucher specimens deposited in the Invertebrate Collection, Royal British Columbia Museum (RBCM), Victoria.

Species	Site	RBCM number, condition and number of specimens
Microphysula cookei	9	000-062-001, dry, 9
	15	000-066-001, dry, 3
Punctum randolphii	10	000-064-001, dry, 2
	9	000-062-002, dry, 3
Pristiloma arcticum	10	000-064-002, dry, 4
Pristiloma chersinella	6	000-063-001, dry, 12
Vertigo columbiana	2	001-045-001, dry, 2
Vespericola columbianus	4	000-065-001, dry, 1

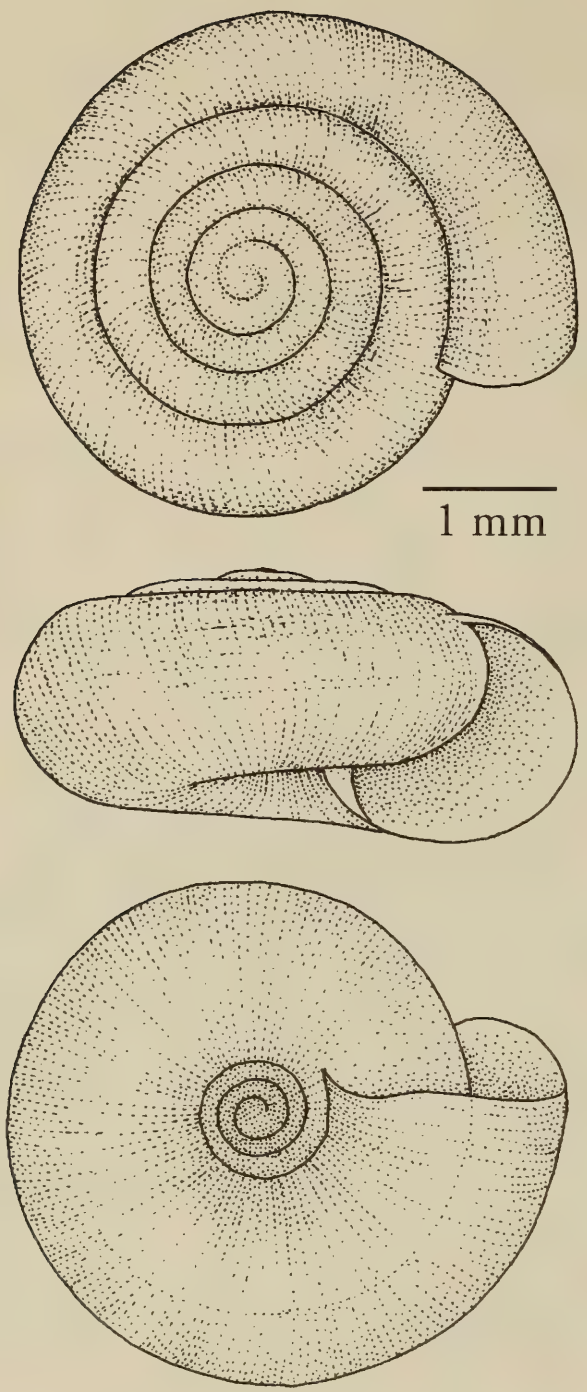

FIGURE 2. *Microphysula cookei*, RBCM 000-062-001, locality 9.

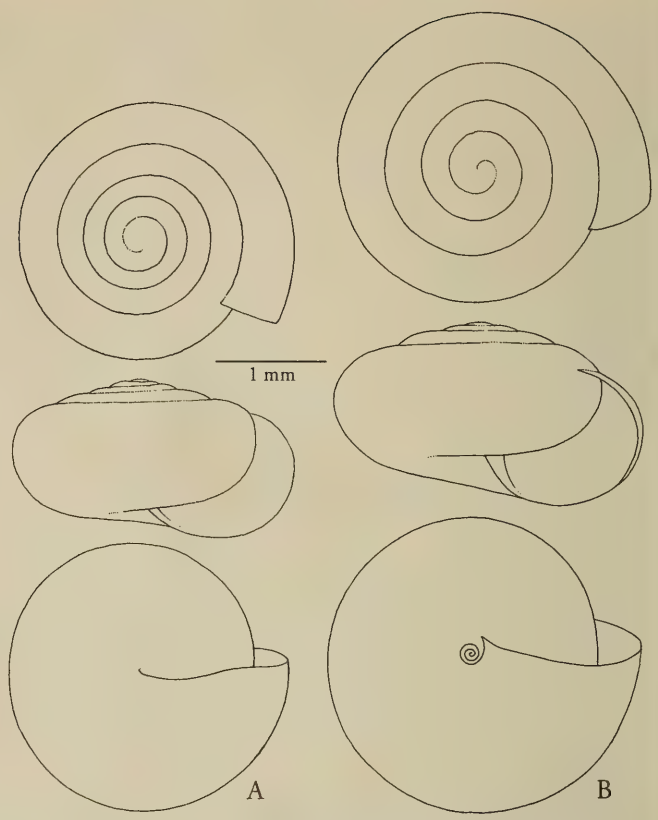

FIGURE 3. *Pristiloma spp.* from the Babine Range, Skeena Mountains. A, *P. arcticum*, RBCM 000-064-002, locality 10. B, *P. chersinella*, RBCM 000-063-001, locality 6.

(1948)] from St. Paul Island, Bering Sea, Alaska. In northern British Columbia, this species has recently been found in the Queen Charlotte Islands (Forsyth, unpublished). I have also collected it from Hyder, southeast Alaska.

The remaining *Vertigo* material is less easily identified. The nomenclature of Nearctic *Vertigo* (see Pilsbry 1948) requires a complete reassessment. However, most specimens resemble *Vertigo modesta parietalis* (Ancey, 1887) more than anything else in the *V. modesta* group. There is also less frequently an elongate, somewhat prominently rib-striate form that appears to intergrade with the more common, stouter and smoother form.

Vespericola columbianus (I. Lea, 1838),
Northwest Hesperian

This is a common snail along the entire coast of British Columbia, extending inland along major river valleys. An empty shell and a fragment were found at sites 4 and 5, respectively, on Hudson Bay Mountain. The discovery of this species on Hudson Bay Mountain was unexpected, since it was not found in the nearby Bulkley Valley. The nearest known valley population of *V. columbianus* is near the confluence of the Suskwa and Bulkley Rivers (55°13.27′N, 127°26.72′W; elevation ca. 300 m), ca. 43 km northwest of Hudson Bay Mountain. Southwest from the mouth of the Suskwa River this species is common along the Bulkley and Skeena Rivers to the coast (personal observation).

Within the genus *Vespericola*, reproductive anatomies are more useful in determining species than conchological characters (Roth and Miller 1993). Roth and Miller mentioned dissected British Columbia material, and they established that *V. columbianus* (but not "*Vespericola columbianus pilosus*", which is a separate species limited to the San Francisco region of California) occurs north of the Columbia River type locality. The identification of

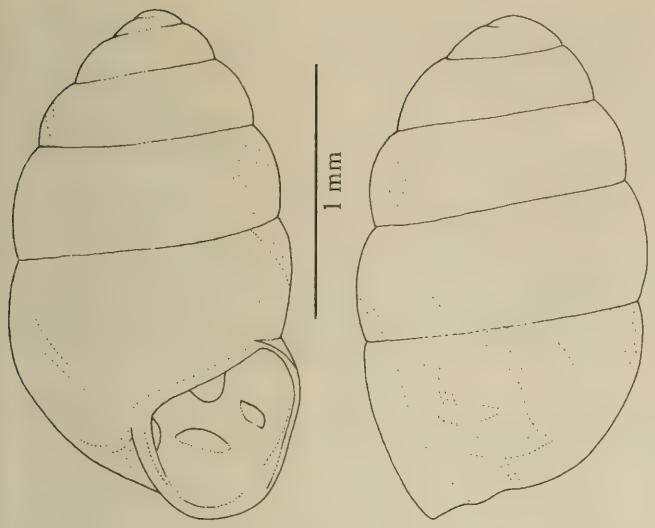

FIGURE 4. *Vertigo columbiana*, RBCM 001-045-001, locality 2.

British Columbia *Vespericola* as *V. columbianus* is provisional in the sense of Roth and Miller (1993), pending anatomical verification. However, dissection of more British Columbia material, including specimens from the Bulkley Range, would be desirable. The Hudson Bay Mountain specimen does not show any shell features obviously different from coastal examples of the species.

Discussion

The terrestrial gastropod fauna of the Babine and Hazelton Ranges is comprised of both inland and coastal elements (Table 2). Of particular interest, *Punctum randolphii*, *Microphysula cookei*, *Vertigo columbiana* and *Vespericola columbianus* appear to be restricted to elevations at and above ca. 900 m and are apparently absent from the nearby Bulkley Valley.

In the vicinity of the study area, precipitation generally decreases from west to east and from higher to lower elevations, and the montane forests receive greater precipitation than does the valley (Banner et al. 1993). Located in the rain shadow of the Coast and Hazelton Mountains, Smithers receives far less precipitation than the coast (512 mm/yr at Smithers compared to 2414 mm/yr at Prince Rupert) and even less than the city of Prince George on the Interior Plateau (650 mm/yr), 300 km to the southeast (Hare and Thomas 1979). Banner et al. (1993), however, described the climate of the northwestern Bulkley Valley as mainly continental with "some lingering coastal influences."

Vespericola columbianus is typically a coastal snail occurring from Unalaska Island, Aleutian Islands (Hanna 1925) and southeast Alaska south to northwestern California (Roth and Miller 1993), living from lowlands to above 1000 m (Branson 1977, 1980). In this study, *V. columbianus* was apparently scarce in the Hazelton Range and not found in the Babine Range. Its apparent absence from the Babine Range might be explained by insufficient sampling, but the Babine Range is also further removed from the coast and has a slightly drier, more continental climate (Banner et al. 1993).

The inland distribution of *V. columbianus* up the Bulkley River Valley to Hudson Bay Mountain appears to be associated with the penetration of humid coastal air from the Coast Mountains. The Suskwa River locality and the area around and to the north and northwest of Hazelton lies near the drier, eastern part of the Interior Cedar-Hemlock biogeoclimatic zone; conditions are much more coastal here than further east up the Bulkley Valley (Banner et al. 1993). At Smithers, the Bulkley Valley is considerably drier and is classified in the Sub-Boreal Spruce zone, but above the Sub-Boreal Spruce zone lies the wetter subalpine forests of the Englemann Spruce-Subalpine Fir zone (Meidinger and Pojar 1991; Banner et al. 1993). It appears that *V. columbianus* is able to extend up the Skeena and Bulkley valleys as far as ample moisture is present, but beyond this its occurrence is limited to wetter subalpine forests. The occurrence of *Punctum randolphii*, *Microphysula cookei* and *Vertigo columbiana* along the North Coast and up the Skeena Valley could follow a similar pattern as *V. columbianus*.

Whereas Cameron (1988) suggested that the eastern limits of coastal species were restricted by the unfavourable alpine environment of high mountains and a radical change in climate on from their windward to leeward sides, it seems likely that these species are not entirely barred from the eastern side of the Coast Mountains by high alpine obstacles. Climatically suitable corridors enable precipitation-dependent coastal species to extend well inland from the coast.

Acknowledgments

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Appendix: Localities

Hudson Bay Mountain, Bulkley Range, Hazelton Mountains:

1 "Crater Lake," 54°47.2′N, 127°18.2′W, R. G. Forsyth and T. J. Forsyth collectors, 19-IX-1996, alpine, under rocks, heather and moss, 1700 m.

2 Glacier Gulch, 54°49.3′N, 127°16.8′W, R. G. Forsyth and T. J. Forsyth collectors, 3-IX-1997, spruce forest with some deciduous trees and shrubs, 1100 m.

3 Toboggan Creek Trail, 54°50.8′N, 127°19.2′W, R. G. Forsyth and T. J. Forsyth collectors, 25-IX-1998, willow, cottonwood, alder, thimbleberry and elderberry in fir-spruce forest, 1100 m.

4 Toboggan Creek Trail, 54°50.7′N, 127°18.1′W, R. G. Forsyth and T. J. Forsyth collectors, 25-IX-1998, rockslide with birch, aspen, cottonwood and fir, 1000 m.

5 Toboggan Creek Trail, 54°50.9′N, 127°17.5′W; R. G. Forsyth and T. J. Forsyth collectors, 25-IX-1998; in leaf litter of willows, aspen, thimbleberry; 900 m.

Babine Range, Skeena Mountains:

6 Little Joe Trail, below Eagle Pass, ca. 54°52.8′N, 126°47.7′W; R. G. Forsyth and T. J. T. Forsyth collectors, 29-IX-1995; under rocks and dead vegetation in old vegetated rockslide at tree line, 1600 m.

7 Astlais Mountain, 54°48.8′N, 126°52.9′W; R. G. Forsyth and T. J. Forsyth collectors, 2-IX-1997; under loose rock at tree line; 1600 m.

8 Astlais Mountain, 54°48.8′N, 126°53.1′W; R. G. Forsyth and T. J. Forsyth collectors, 2-IX-1997; under loose rock near tree line; 1400 m

9 Astlais Mountain, 54°48.4′N, 126°53.1′W; R. G. Forsyth and T. J. Forsyth collectors, 2-IX-1997; under rocks and dead wood in spruce forest; 1200 m.

10 Silver King Basin Trail, 54° 53.7′N, 126°54.1′W; R. G. Forsyth and T. J. Forsyth collectors, 29-IX-1998; on mossy, leaves, rocks and dead wood, in spruce forest; 1300 m.

11 Silver King Basin Trail, 54° 53.5′N, 126°56.1′W; R. G. Forsyth and T. J. Forsyth collectors, 29-IX-1998; under rocks in run-off area with willows, alders, spruce and cow parsnip; 1200 m.

12 Silver King Basin Trail, 54° 53.5′N, 126°57.1′W; R. G. Forsyth and T. J. Forsyth collectors, 29-IX-1998; spruce, cow parsnip, horsetail; 1100 m.

13 Dome Mountain Trail, 54°46.2′N, 126°47.2′W; R. G. Forsyth and T. J. Forsyth collectors, 1-IX-1998; burn area with young conifers; in leaf litter of willow and other dead plant material, 1100.

Nechako Plateau, Interior Plateau:

14 Tsezakwa Creek at Nilkitkwa Forest Service Road, near km 44, W of Fort Babine, 55°19.1′N, 126°39.8′W, R. G. Forsyth and T. J. Forsyth collectors, 6-IX-1997, disturbed roadside, young cottonwoods, ca. 730 m.

Bear River Pass, Boundary Range, Coast Mountains:

15 Rest stop overlooking east end of Strohn Lake, Hwy. 37A (Stewart Hwy.), ca. 56°02.2′N, 129°39.0′W; R. G. Forsyth and T. J. Forsyth collectors, 28-IX-1995; alder-cottonwood scrub; ca. 460 m.

The Establishment and Proliferation of the Rare Exotic Plant, *Lythrum hyssopifolia*, Hyssop-leaved Loosestrife, at a Pond in Guelph, Ontario

Marc T. Johnson[1], and Carl J. Rothfels[2]

[1]Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2 Canada; email: johnson@botany.utoronto.ca [author for correspondence]
[2]R.R. 1, Pefferlaw, Ontario L0E 1N0 Canada

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Understanding the biology of exotic species and their potential to be invasive is of interest to both theoretical and applied ecologists. We studied the establishment and proliferation of the exotic *Lythrum hyssopifolia*, Hyssop-leaved Loosestrife, over three years (1998 to 2000) at a recently dug pond in the city of Guelph, Ontario. This location is the second record of the species in Ontario. In each year we recorded the location of plants, the number of stems and their density within discrete sites. In 1998 we found a single plant with 15 stems that bore numerous flowers and mature fruits. By 2000, plants were growing at 10 discrete sites around the pond; there were an estimated 1 556 plants giving rise to a total of 2090 stems. Although *L. hyssopifolia* may become more frequent in Guelph and Ontario, it is unlikely that it will be as abundant and invasive as its congener *Lythrum salicaria*, Purple Loosestrife.

Key Words: *Lythrum hyssopifolia*, Hyssop-leaved Loosestrife, non-native, exotic, alien, introduced, biological invasions, rarity, establishment, population growth.

Understanding the biology of exotic plant species is of major interest for ecologists, largely because of the ability of some exotic species to compete with and displace native and agricultural ones (Holm et al. 1977; D'Antonio and Mahall 1991; US Congress 1993; Williamson and Fitter 1996; Vitousek et al. 1996). Much effort has been made to determine which exotic species will successfully invade and where they will become pests (Lodge 1993; Williamson 1996; Crawley et al. 1996; Reichard and Hamilton 1997; Horvitz et al. 1998; Kotanen et al. 1998). Theoretical models have been formulated (Watkinson 1986; Higgins and Richardson 1996; Williamson 1996) and empirical studies have tested these theories of invasion (Crawley et al. 1996; reviewed in Williamson 1996; Kotanen et al. 1998). As a result, there are now generalized conceptual frameworks on biological invasions (Lodge 1993; Williamson 1996), as well as statistical generalizations on the habitats and traits most often associated with exotic species (Crawley et al. 1996; Kotanen et al. 1998). Despite these advancements, predicting the future outcome of a specific introduction remains difficult (Lodge 1993; Williamson 1996). Generalized predictions are possible if observations are made on the initial processes of an introduction (whether or not establishment occurs; fecundity; rate of population increase; rate of spread; and community interactions) and these data are coupled with further knowledge of life history traits of the species (Williamson 1996). To do this, one must witness the initial stages of an introduction , which we have done with *Lythrum hyssopifolia* L. (Lythraceae), Hyssop-leaved Loosestrife, a rare exotic in Canada.

Lythrum hyssopifolia is a summer annual; details of its morphology and identification can be found in Gleason and Cronquist (1991) and Callaghan (1998). *Lythrum hyssopifolia* can cross-fertilize, but it readily self-pollinates (Preston and Whitehouse 1986; Callaghan 1998). Plants can increase in numbers rapidly because they produce copious seeds as well as new clonal shoots from adventitious roots (Callaghan 1998). Originally an Old-World species, *L. hyssopifolia* is now found on every continent except Antarctica (Callaghan 1998). It was first recorded in North America from Boston in ca. 1815 (Shinners 1953) and now occurs frequently on the west coast of the United States and on the east coast from Maine to New Jersey and eastern Pennsylvania (Steere 1966; Gleason and Cronquist 1991). Inland there are historic records from Detroit, Michigan (Voss 1985) and southern Ohio (Gleason and Cronquist 1991; S. Graham, personal communication), which are discussed in detail by Blaney et al. (1997). To our knowledge, *L. hyssopifolia* is only known from three localities in Canada. The first record was a collection made in 1992 from a farmer's field north of Belleville, Ontario (Blaney et al. 1997). Since 1992, *L. hyssopifolia* has also been reported in Canada from two locations in British Columbia: Vancouver Island and south-central British Columbia (Douglas et al. 1998; Douglas et al. 1999).

Lythrum hyssopifolia appears characteristically in areas that are periodically flooded in winter and

spring, are frequently disturbed, and contain few other plants (Preston and Whitehouse 1986; Bliss and Zedler 1998; Callaghan 1998). Commonly a pioneer of exposed soil, it does well in arable fields that are moist or experience periodic flooding (Blaney et al. 1997; Callaghan 1998). *Lythrum hyssopifolia* can proliferate quickly if conditions are favourable for its growth, but populations are also prone to precipitous decline (Preston and Whitehouse 1986; Callaghan 1998). Despite these population fluctuations, *L. hyssopifolia* is somewhat protected from local extirpation by the long-lived seed bank characteristic of this species (Preston and Whitehouse 1986).

We report the results from a three-year observational study of a population of *L. hyssopifolia* in Guelph, Ontario, Canada. These observations document the establishment from the presumed first reproducing plant in the population, followed by the proliferation of this species in a localized area. Our discovery of *L. hyssopifolia* in Guelph represents the second record of this species in Ontario (Blaney et al. 1997), the fourth in Canada (Douglas et al. 1999).

Methods

All observations and data were collected in the mid-summer or fall of 1998, 1999 and 2000. The study site was an artificial pond in the south-west section of the city of Guelph, Ontario, 43° 30.6′ N, 80° 13.1′ W, which is south-west of the intersection of Edinburgh Rd. and South Creek Trail, between "Preservation Park" (the south and west border of the pond) and a subdivision constructed in 1996 (the north border of the pond).

The pond was dug in 1995 or 1996 as part of a series of ponds scattered throughout Guelph to capture overflow from suburban storm gutters (Guelph Public Works Commission, personal communication). The pond measures approximately 145 m (east-west) by 85 m (north-south) (Figure 1). It contained water throughout the study and has probably contained water since its creation, although the water level fluctuated within and between years of our study. A band of exposed soil narrowly lined the perimeter of the pond, but changed in width as the water level fluctuated. The width of the exposed soil narrowed from 1998 to 2000 as perennial species increased in abundance around the pond's margin.

The plant community at the pond was typical of species associated with exposed water-saturated soil as well as old fields (see Results for a list of most common species).

Sampling

Lythrum hyssopifolia was first discovered on 2 October 1998. On this date the pond's margin was searched for additional plants. On 6 October of the same year, the margin of the pond was searched again. Neither search located any additional plants, nor were any found in nearby ponds.

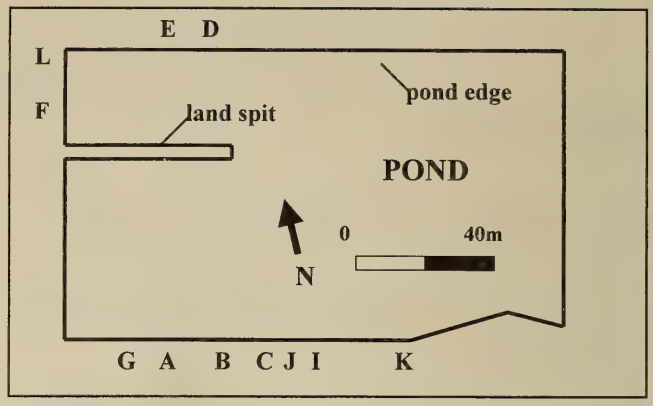

FIGURE 1. Diagram of the pond where *Lythrum hyssopifolia* was observed. Letters A through L represent discrete locations at the pond's edge where plants were found between 1998 and 2000. In 1998, a single *L. hyssopifolia* plant found was found at site A. In 1999, *L. hyssopifolia* plants were found at seven sites, A-G. In 2000, *L. hyssopifolia* plants were found at 10 sites, A-L; except E and G.

On 7 October 1999 and 31 July and 1 August 2000, the pond was revisited and the exposed soil at the pond margin and 1m back in thicker vegetation were searched to locate *L. hyssopifolia* plants. Discrete sites separated by at least 3 m between plants were delineated and the numbers of stems within each site were counted. Stems were counted instead of the number of plants because prolific branching, high stem densities and clonal propagation made the identification and counting of individual plants impractical. If it was obvious that a single plant contained branches, the branches were recorded as "stems" provided that the branching occurred at the base of the plant. Counting each aggregation of stems as a single plant made a conservative estimate of the number of plants. Stem densities (stems/m^2) were calculated for sites with multiple "plants". In 1998 and 1999, the number of stems bearing fruits or flowers were counted, but this was not done in 2000 since most stems were not yet in flower on the sampling date.

Results

The single *L. hyssopifolia* plant observed in October 1998 was composed of 15 branches, each 20–40 cm long, that diverged at the plant base. These branches bore numerous flowers (in the apical leaf axes) and fruits (present nearly to the base of the stems). One stem that was collected (now deposited at OAC, see below) had 25 flowers and 28 mature fruits. Many smaller stems (less than 5 cm in length) were present at the base of the plant. Two of the larger branches were collected and are now deposited at Kent State University in Dr. Shirley Graham's personal Lythraceae research herbarium (*M.T. Johnson s.n. & C. J. Rothfels*, KE-Graham) and the

University of Guelph Herbarium (*M.T. Johnson s.n. & C. J. Rothfels*, OAC).

In October 1999, *L. hyssopifolia* was found at seven sites around the margin of the pond (Figure 1). Among the seven sites, we estimated a total of 100 individual plants and counted 426 stems, of which 292 (69%) bore either fruits or flowers. The number of stems in a site ranged from 1 to 252, while the number of fruiting/flowering stems ranged between 0 and 201. Densities of stems at sites A, C and D, ranged from 68.6 stems/m^2 to 187.0 stems/m^2 (Table 1), but within site D one area had 166 stems at a density of 319 stems/m^2. Most plants grew in the exposed soil or were rooted in soil but partially submerged. A smaller number grew in more dense vegetation, but never far from the edge of the exposed soil.

Many stems bore mature fruit, but some stems appeared to have shed entire fruits; fruits fell away when gently manipulated by hand. We also observed that parts of stems were missing from some plants, possibly broken off or consumed.

In July 2000, *L. hyssopifolia* plants were at 10 sites around the pond, four of which were new (Figure 1). Among these sites were an estimated 1556 plants and 2090 stems. Some stems had begun to flower, but none bore mature fruits. The number of stems within a site ranged from 1 to 1 487 (Table 1). Stem density was calculated at 6 sites and ranged from 157 stems/m^2 to 2750 stems/m^2 (Table 1), but stem density of immature plants was recorded as high as 10 500 stems/m^2 in a 0.1 m × 0.1 m quadrat. As in 1999, all stems were found at the pond's margin, but unlike the previous year no plants were found in the more heavily vegetated areas. All stems grew within a 0.6 m band of exposed soil around the pond.

TABLE 1. The sites (A-L) where *Lythrum hyssopifolia* plants were found, the number and density (stems/m^2) of stems (for sites with more than a single "plant") in 1999 and 2000. The total number of stems among all sites is also included. Sites that contained at least one stem with fruit or flower in 1999 are indicated by an *. In 1998 there was only a single plant with 15 stems, located at site A.

	Number of Stems		Stem Density (stems/m^2)	
Site	1999	2000	1999	2000
A	36*	31	69	157
B	2*	44		2750
C	118*	409	171	228
D	252*	1487	187	292
E	14	0		
F	3*	101		28
G	1	0		
H	0	1		
I	0	4		
J	0	1		
K	0	11		550
L	0	1		
All	426	2090		

*at least one stem in flower/fruit.

Discussion

The single plant of *L. hyssopifolia* found in 1998 was likely the first fertile individual to occur at this site, because the pond was only 2-3 years old, and *L. hyssopifolia* is an annual that can increase in numbers rapidly when colonizing exposed soil (Preston and Whitehouse 1986; Callaghan 1998; Bliss and Zedler 1998). Therefore, we would have expected more than a single plant in 1998 if fruiting plants had previously existed in the area. Although its mode of transportation to the pond is unknowable, seeds could have been transported on birds' feet or in feces.

There was a large proliferation of *L. hyssopifolia* around the pond from 1998 to 1999 (Table 1). Either seeds from the 1998 plant dispersed and germinated at the sites found in 1999, or a seed bank was present in 1998 that did not germinate until 1999. These hypotheses are not necessarily mutually exclusive. We believe that the first hypothesis best explains the population structure observed in 1999 and 2000. This hypothesis would be improbable if only independent dispersal of individual seeds accounted for the distribution of all stems in 1999. It is not improbable, however, if entire fruits and/or branches containing fruits were dispersed to these sites. We did observe stems in which fruits appeared to have been shed and branches were broken off. Preliminary tests confirm that fruits are buoyant. Despite this, we cannot completely dismiss the second hypothesis – proliferation due to the germination of a seed bank. *Lythrum hyssopifolia* is known to form seed banks (Bliss and Zedler 1998) and seeds can remain dormant for many years prior to germination (Preston and Whitehouse 1986). Since the habitat in 1998 appeared ideal for *L. hyssopifolia* we would have expected more plants in 1998, but only one plant was found, therefore the presence of a large seed bank prior to 1998 is unlikely.

From 1999 to 2000 there was an increase in the number of sites, plants, and stems, as well as an increase in stem density (Table 1). This increase is not surprising based on the amount of available habitat and the number of stems fruiting in 1998 and 1999. It is surprising, however, that only four additional sites were found between 1999 and 2000 and none of these sites contained more than 11 stems.

This is in contrast to the colonization pattern observed from 1998 and 1999.

The habitat at the site was consistent with the habitats reported from other populations of *L. hyssopifolia*: anthropogenic disturbance, fluctuating water levels, annual-dominated zone (Steere 1966; Tutin et al. 1968; Preston and Whitehouse 1986; Blaney et al. 1997; Bliss and Zedler 1998; Callaghan 1998). The vascular flora around the pond was similar to other studies (Preston and Whitehouse 1986; Callaghan 1998). The most common species* were *Anagallis arvensis* (Pimpernel), *Euthamia graminifolia* (Grass-leaved Goldenrod), *Juncus bufonius* (Toad Rush), *Juncus dudleyi* (Dudley's Rush), *Juncus effusus* (Soft Rush), *Lolium* spp. (Ryegrass), *Panicum capillare* (Witch Grass), *Plantago major* (Common Plantain), *Trifolium hybridum* (Alsike Clover) and *Typha angustifolia* (Narrow-leaved Cattail).

The data collected in this study can be related to theoretical conceptual frameworks on exotic species and biological invasions (Lodge 1993; Williamson 1996). On the one hand, *L. hyssopifolia* has traits traditionally attributed to many invasive exotic species (Lodge 1993): r-selection; annual; self-reproduction; high dispersal rate; vegetative reproduction and human commensalism. It also occurs in ruderal habitats with low species diversity, a characteristic of many exotics (Lodge 1993; Crawley et al. 1996). On the other hand, it has traits that are not consistent with recent generalizations made about exotic species (Crawley et al. 1996). Crawley et al. (1996) found that exotic taxa were significantly more likely to have larger seeds, perennial growth, taller shoots, cross-pollinated reproduction and earlier flowering. The reverse is true for each of these traits if we compare *L. hyssopifolia* with its native congener, *L. alatum* (Winged Loosestrife). Although Crawley et al. (1996) were using data from the British flora and based their conclusions on robust statistical tests, it should be noted that their conclusions are a rule of thumb and exceptions exist.

Closely related species often have traits that covary (Felsenstein 1985). Because of this covariation the invasive ability of related exotic species may be similar (Crawley et al. 1996; Kotanen et al. 1998), and potentially used as a predictor of invasion (Williamson 1996). A comparison between *L. hyssopifolia* and its congener *Lythrum salicaria* (Purple Loosestrife) provides a test of this prediction. *Lythrum salicaria* is known as an invader of wetlands and mesic habitats in North America, although its ability to displace other organisms is under debate (Anderson 1995; Hager and McCoy 1998). *Lythrum hyssopifolia* is potentially a minor pest in some circumstances (Blaney et al. 1997; Callaghan 1998), but its ecological requirements are more restricted than those of *L. salicaria*, and therefore it has not proliferated in North America as successfully as *L. salicaria*, especially at northern latitudes. It is clear that the invasive ability of these congeners is not equal. *L. hyssopifolia*'s smaller size, high self-pollination rate and its annual growth habit may all contribute to this difference in invasive ability. The difference in invasive ability between the two species supports Williamson's belief (1996) that the differences between related taxa are more important than their similarities, which suggests relatedness can not be used reliably as a predictor of invasiveness.

Prognosis

What will happen to *L. hyssopifolia* in the Guelph area and will it spread further in Ontario? It is likely that *L. hyssopifolia* will become more frequent in Guelph and elsewhere in Ontario, but unlike its congener, *L. salicaria*, it will rarely be common or displace native plant species. Four points support this prediction. First, *L. hyssopifolia* has specific habitat requirements (i.e. periodically flooded ruderal areas and arable fields) that typically have a low density and diversity of native species (Preston and Whitehouse 1986; Bliss and Zedler 1998; Callaghan 1998). Second, *L. hyssopifolia* appears to compete poorly with perennials (Preston and Whitehouse 1986; MTJ, unpublished data). Third, *L. hyssopifolia* is usually rare in north-temperate climates like that of southern Ontario, even if small populations persist for many years (Tutin et al. 1968; Blaney et al. 1997; Callaghan 1998; Douglas et al. 1999). Finally, despite a long history of introductions in eastern North America, this species has so far failed to establish abundant inland populations.

We suspect that *L. hyssopifolia* will remain restricted to ruderal habitats including vernal pools, ponds and waterways with exposed soil, or arable land that is frequently ploughed and contains areas with winter/spring flooding. The status of *L. hyssopifolia* in Canada should continue to be monitored and further research should concentrate on determining the ability of *L. hyssopifolia* to compete with and displace other plant species as well as its potential to act as an agricultural pest.

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*Nomenclature follows Morton and Venn (1990) for all species except *L. hyssopifolia* for which Gleason and Cronquist (1991) was used.

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Records of Canada Lynx, *Lynx canadensis*, in the Upper Peninsula of Michigan, 1940–1997

Dean E. Beyer, Jr.[1], Brian J. Roell[1], James H. Hammill[2], and Richard D. Earle[3]

[1]Michigan Department of Natural Resources, Wildlife Bureau, Marquette, Michigan 49855 USA
[2]Michigan Department of Natural Resources, Wildlife Bureau, Crystal Falls, Michigan 49920 USA
[3]Michigan Department of Natural Resources, Wildlife Bureau, Houghton Lake, Michigan 48629 USA

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We compiled 62 records of Lynx occurrence in Michigan's Upper Peninsula from 1940–1997. Thirty-nine of the Lynx records were verified by biologists. The last specimen was reported in 1983 and the last verified track was found in 1996. Over 50% of Lynx occurrences were reported in the 1960s. These occurrences appear to be the result of Lynx dispersing from Canada after a population irruption. Extensive track count surveys for Gray Wolves (*Canis lupus*) and other furbearers have yielded no evidence of Lynx. We conclude that Lynx are absent or extremely rare at this time and found no evidence that supports the existence of a resident population.

Key Words: Canada Lynx, *Lynx canadensis*, Michigan, records.

Historically, Canada Lynx (*Lynx canadensis*) were residents of the Upper Peninsula of Michigan (Baker 1983; U.S. Fish and Wildlife Service 1998). Lynx are most commonly associated with the boreal forest ecosystem (McCord and Cardoza 1982; Quinn and Parker 1987). The Upper Peninsula is near the southern edge of the lynx's range and is in an area of transition from boreal forest to northern hardwoods. The distribution of lynx closely agrees with the distribution of its primary prey, Snowshoe Hares (*Lepus americanus*), and lynx and hare populations in the northern boreal forest follow an approximate 10-year cycle (Elton and Nicholson 1946; Keith 1963). The dynamics of lynx populations at the southern end of their range are not well understood (Ruggiero et al. 1999).

It is not clear if lynx were extirpated from the Upper Peninsula. Harger (1965) reported a gap of 26 years, from 1913 to 1939, when no sign of lynx was recorded. However, Wood (1917) reported that lynx were present in Alger County in 1916 and Baker (1983) reported a specimen trapped in Ontonagon County in 1928. The ninth Biennial Report (1937-1938) of the Michigan Department of Conservation indicated that lynx were rare and possibly extinct in Michigan (Michigan Department of Conservation 1938). However, Baker (1983) and Harger (1965) both pointed out that an occasional lynx may have immigrated from Canada to the eastern Upper Peninsula by crossing the St. Mary's River. Pruitt (1951) reported an observation of lynx tracks on Sugar Island in the St. Mary's River during the winter of 1949–1950.

Harger (1965) reviewed the status of lynx in Michigan, especially records of the animal in the Upper Peninsula from 1940–1962. Harger reported that 12 lynx were killed in the Upper Peninsula in 1962. He suggested the number and the peninsula-wide distribution of these records indicated that lynx were repopulating the Upper Peninsula. However, Thiel (1987) concluded that increased lynx numbers in Wisconsin at this same time were the result of immigration following a massive population irruption of lynx in Canada in 1961. Furthermore, Thiel found associations between lynx population irruptions in Canada and number of lynx specimens collected in the Upper Great Lakes states (Michigan, Minnesota, and Wisconsin) from 1856– 1980.

The lynx was listed by the Michigan Department of Natural Resources as a state threatened species in 1983. In 1987, the lynx's status was changed to state endangered. National Forests located in the Upper Peninsula (Hiawatha and Ottawa) list the lynx as a sensitive species. In April 2000, the Fish and Wildlife Service listed the contiguous United States population segment of lynx as a Federally threatened species (U.S. Fish and Wildlife Service 2000). This listing includes all of the Great Lake states. Federal listing necessitates increased consideration of lynx in land management planning and implementation, especially on Federal Lands.

In this paper, we present a compilation of lynx records for the Upper Peninsula of Michigan from 1940–1997. We also present data from recent track count surveys throughout the Upper Peninsula that suggests lynx are absent or extremely rare at this time.

Methods

Lynx Records

We surveyed the Michigan Department of Natural Resources, Hiawatha and Ottawa National Forests,

Seney National Wildlife Refuge, and Picture Rocks National Lakeshore for records of lynx occurrence in the Upper Peninsula. These public land management agencies are directly responsible for managing wildlife and wildlife habitat on 1 648 552 ha of the Upper Peninsula. The Michigan Department of Natural Resources is also responsible for managing wildlife populations on private lands throughout the state. We also surveyed three large industrial forest landowners and an environmental consulting firm that conducts wildlife surveys in the Upper Peninsula. Finally, we contacted museums at Michigan State University and the University of Michigan to determine if they had records not compiled by Harger (1965).

For all lynx records, we report the type of record as specimen, track, or sighting. We also determined the date, location, and the observer. For specimens, we noted the sex, weight, and archive location when available. We also made a determination of whether a record had been verified. We considered a record verified if the specimen or track was inspected by a biologist or if a photograph (specimens) was available for inspection. Unverified records were those specimens and tracks not physically examined by a biologist. All lynx sightings were considered unverified. However, biologists recording sightings of lynx or tracks routinely question the observer to ensure, to the extent possible, that a sighting or track was actually a lynx.

We created a geographic information system point coverage of records that were described by U.S. Land Survey Units (Township, Range, and Section). The point representing each record was located in the center of the referenced Section. We created a map to view the spatial distribution of lynx records.

Track Surveys

Prior to the 1990s, no systematic surveys were conducted to determine if lynx were present, and if present, their distribution. In the 1990s the Michigan Department of Natural Resources initiated two independent track count surveys in the Upper Peninsula. A Gray Wolf (*Canis lupus*) track count survey was started in 1992 and a furbearer track count survey was begun in 1997. Personnel trained in track identification conducted both surveys. The wolf track count survey was conducted during winter, primarily January through March, and involved extensive and intensive searches of roads and trails for wolf sign. Roads and trails were systematically searched for sign using snowmobiles and 4-WD trucks. Although this survey was primarily designed for wolves, observers were instructed to record tracks of other rare predators when encountered.

The furbearer track count survey was designed to determine the distribution and abundance of Marten (*Martes americana*) and to assess the potential of using this approach to monitor other furbearer populations. The furbearer track count survey was conducted along survey routes comprised of four segments, each approximately 8 km in length. Distances of 4 to 8 km separate segments of each route. Routes were established on unpaved roads and trails. Routes were surveyed once during January–March using snowmobiles or 4-WD vehicles.

Results and Discussion

Lynx Records

Including Harger's (1965) 1940–1962 records, there have been 62 reports of lynx occurrence in the Upper Peninsula from 1940–1997 (Table 1). These records include 39 specimens, 16 tracks, and seven sightings. Fifty-five of the record locations were described in Land Survey Units, and the remaining seven observations were described by county of occurrence. Biologists verified 33 of the 39 specimens. Six of 16 tracks reported were inspected or reported by a biologist. None of the seven sightings were verified.

The number of records per decade was relatively consistent, except during the 1960s when 37 reports were compiled (Figure 1). The increase in the 1960s was consistent with increases in Wisconsin and Minnesota and appeared related to a population irruption and subsequent population crash in Canada and an influx of dispersing animals (Thiel 1987). Another population irruption in Canada in the early 1970s resulted in increased reports of lynx in Minnesota and Wisconsin (McKelvey et al. 1999a), but this increase was not observed in the Upper Peninsula of Michigan. Fragmentation of habitat in southern Quebec may have reduced the number of dispersal routes for lynx emigrating to New York, Vermont, and New Hampshire (Litvaitis et al. 1991; U. S. Fish and Wildlife Service 1998). The status of dispersal routes into the Upper Peninsula has not been studied.

The last specimen reported was a 9.5 kg male that was trapped in Mackinac County in 1983. Since 1981, there has been mandatory registration of Bobcats (*Felis rufus*) in Michigan under the Convention for International Trade in Endangered Species of Wild Fauna and Flora Treaty. lynx are reported to be susceptible to trapping (Ruggiero et al. 1999). However, the 1983 Mackinac County specimen has been the only lynx checked in the Bobcat harvest to date. The last verified record of lynx was a track found in Iron County in 1996. The last record of lynx in the Upper Peninsula was an unverified track in Dickinson County in 1997. Six reports of lynx were made in the 1990s; five track records and one sighting. Three of the six records came from a relatively small area — about 10 km^2 in Dickinson County in 1996 and 1997. It is possible that all of these records were from a single animal that survived for a few years.

Lynx were reported in nine of 15 counties in the Upper Peninsula (Figure 2). Lynx emigrating from

TABLE 1. Records of lynx in the Upper Peninsula of Michigan, 1940–1997.

Year	Record type	Verified	Sex	Weight (kg[1])	County	Latitude	Longitude	Archive location[2] specimen number
1940	Specimen	Yes			Mackinac	45.743	-84.434	
1940	Specimen	No			Mackinac	45.743	-84.455	
1940	Specimen	No			Mackinac	45.743	-84.455	
1946	Sighting	No			Marquette			
1949	Specimen	No			Mackinac			
1950	Tracks[3]	No			Chippewa			
1953	Specimen	Yes	M	11.8	Chippewa	46.340	-84.228	UMMZ #100811
1955	Specimen	Yes	F	7.3	Marquette			GRPM #83297
1957	Tracks	Yes			Marquette			
1958	Specimen	Yes	M	*~9.1*	Mackinac	46.064	-84.291	MSUM #2842
1959	Tracks	Yes			Chippewa	46.267	-84.394	
1960	Specimen	Yes		11.3	Mackinac	46.036	-84.312	
1960	Specimen	Yes	F		Chippewa	46.282	-85.124	MSUM #5860
1960	Tracks	Yes			Chippewa	46.021	-84.103	
1961	Tracks	Yes			Schoolcraft	46.353	-86.251	
1961	Specimen	Yes	F	8.2	Chippewa	46.223	-84.478	UMMA #111169
1961	Specimen	Yes	F	11.3	Chippewa	46.296	-84.582	
1962	Specimen	Yes	M	10.4	Chippewa	46.138	-84.124	
1962	Specimen	Yes	F	*~11.3*	Mackinac	46.050	-84.561	
1962	Specimen	Yes		8.6	Dickinson	46.182	-87.982	
1962	Specimen	Yes	F	11.3	Dickinson	45.921	-88.085	
1962	Specimen	Yes		14.5	Dickinson	46.066	-88.086	
1962	Specimen	Yes	F		Ontonagon	46.672	-89.687	
1962	Specimen	Yes	M	10.9	Chippewa	46.325	-84.228	MSUM #7754
1962	Specimen	Yes	F	11.3	Chippewa	46.180	-84.895	
1962	Specimen	Yes	M	12.2	Schoolcraft	45.977	-85.876	
1962	Specimen	Yes	F	12.7	Chippewa	46.325	-84.499	
1962	Specimen	Yes	F	8.2	Chippewa	46.484	-84.395	MSUM #8002
1962	Specimen	Yes	F	*~10.4*	Ontonagon	46.571	-89.438	
1963	Specimen	No		*~11.3*	Chippewa	45.933	-83.543	
1963	Specimen	Yes	F	*~11.3*	Chippewa	46.499	-85.188	
1963	Specimen	Yes	F	8.2	Chippewa	46.310	-84.499	
1964	Specimen	Yes	F	10.0	Chippewa	46.384	-84.207	
1964	Specimen	Yes	F	5.4	Chippewa	46.470	-84.165	
1965	Specimen	No			Marquette	46.485	-87.562	
1966	Tracks	No			Chippewa	45.963	-83.791	
1966	Specimen	Yes	F		Chippewa	46.267	-84.270	
1966	Specimen	Yes	F	9.5	Marquette	46.600	-87.918	
1966	Specimen	Yes	F	12.7	Schoolcraft	46.382	-86.188	MSUM #12362
1966	Sighting	No			Marquette	46.022	-87.419	
1966	Specimen	Yes			Iron	46.152	-88.544	
1966	Specimen	No			Ontonagon	46.830	-89.155	
1967	Tracks	No			Marquette	46.036	-87.419	
1967	Sighting	No			Iron	46.182	-88.585	
1967	Specimen	Yes	F	9.1	Chippewa	46.296	-84.603	
1968	Tracks	No			Delta	46.093	-86.876	
1968	Tracks	No			Delta	46.021	-86.605	
1969	Sighting	No			Gogebic			
1971	Specimen	Yes			Marquette	46.384	-87.919	
1972	Specimen	Yes			Marquette	46.528	-87.562	
1972	Specimen	Yes	M		Iron	46.239	-88.461	
1976	Tracks	No			Chippewa	46.426	-84.520	
1983	Specimen	Yes	M	9.5	Mackinac	46.107	-84.561	
1983	Tracks	Yes			Iron	46.312	-88.232	
1986	Sighting	No			Iron	45.993	-88.273	
1988	Sighting	No			Iron	46.181	-88.502	
1993	Tracks	No			Iron			
1996	Tracks	Yes			Iron	46.022	-88.772	
1996	Tracks	No			Dickinson	46.210	-87.940	
1997	Tracks	No			Dickinson	46.210	-87.940	
1997	Tracks	No			Dickinson	46.196	-87.961	
1997	Sighting	No			Dickinson	46.124	-88.086	

[1]Weights with "~" and in *italics* are estimated.
[2]UMMZ, University of Michigan Museum of Zoology; UMMA, University of Michigan Museum of Anthropology; MSUM, Michigan State University Museum; GRPM, Grand Rapids Public Museum.
[3]Record reported by Pruitt (1951).

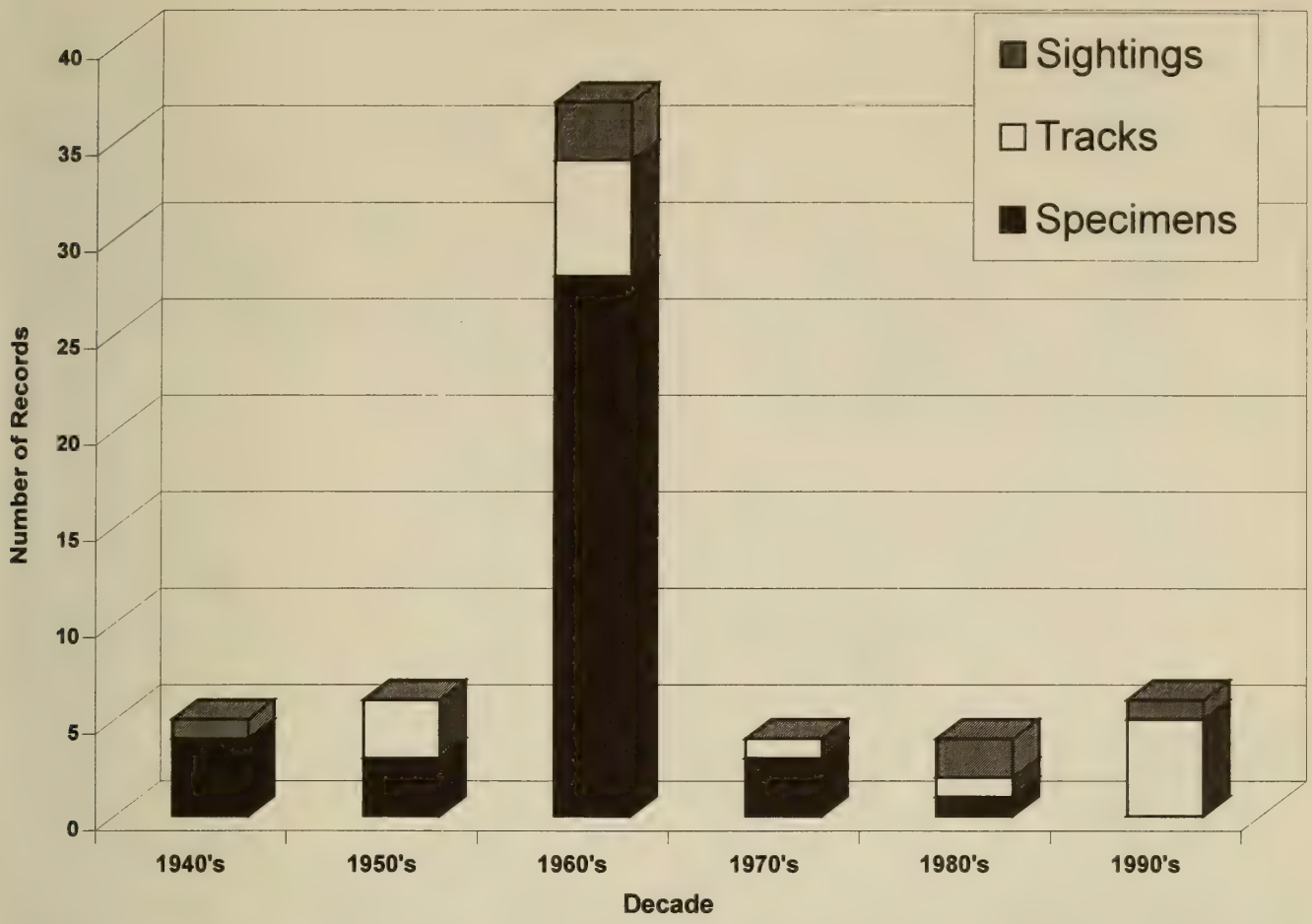

FIGURE 1. Number and type of record of Canada Lynx occurrences in Michigan's Upper Peninsula by decade, 1940–1997.

Canada have two routes into the Upper Peninsula. The long route is through Minnesota and Wisconsin to the western Upper Peninsula. The short route is to cross the St. Mary's River on the east end of the Upper Peninsula. Given the differing lengths of these two routes it is not surprising Chippewa County had more than twice as many records as any other county. Lynx have been reported in the eastern counties of the Upper Peninsula in every decade since the 1940s, except the 1990s. These observations are consistent with the suggestion that the eastern Upper Peninsula is an important entry point for lynx dispersing from Canada. The number of lynx available to disperse into the eastern Upper Peninsula will depend on lynx population levels in Ontario; lynx populations in Canada have been depressed because of overharvesting during the 1970s and 1980s (U. S. Fish and Wildlife Service 1999). The ability of lynx to disperse from Ontario to the eastern Upper Peninsula will depend on the maintenance and connectivity of suitable habitat on both sides of the St. Mary's River.

Of the 26 specimens that were sexed, 19 were females and seven were males. Twenty-one of these specimens (18 females and three males) were collected from 1960–1967. Adult male and female lynx appear to disperse at approximately the same rate (Mech 1980; Slough and Mowat 1996; Poole 1997). Rates of dispersal by juvenile males and females have not been well-documented (Mowat et al. 1999). Very few of the lynx specimens collected in the Upper Peninsula were aged, however, most of the specimens that were weighed appeared to be adults. Mech (1980) felt that both sexes emigrated from Canada to Minnesota in equal numbers. But he found a preponderance of females captured or recovered in Minnesota the year following a large immigration from Canada. Mech attributed the skewed sex ratio to higher mortality rates of males. Given the results from other areas, it is not clear why there are more females in the Upper Peninsula records.

There are two unverified records of possible lynx reproduction in the Upper Peninsula. Two kittens were reported to be trapped on Boise Blanc Island in Lake Huron in 1940. Both specimens were discarded before they could be examined. However, an adult lynx trapped in the same area at the same time was verified. In 1976, tracks of an adult lynx and two kittens were reported in Chippewa County. Unfortunately, neither of these reports were well documented. Even if these records are accurate, they do not prove that breeding and parturition took place in the Upper Peninsula. It is possible that the pregnant females or females and young dispersed from Canada.

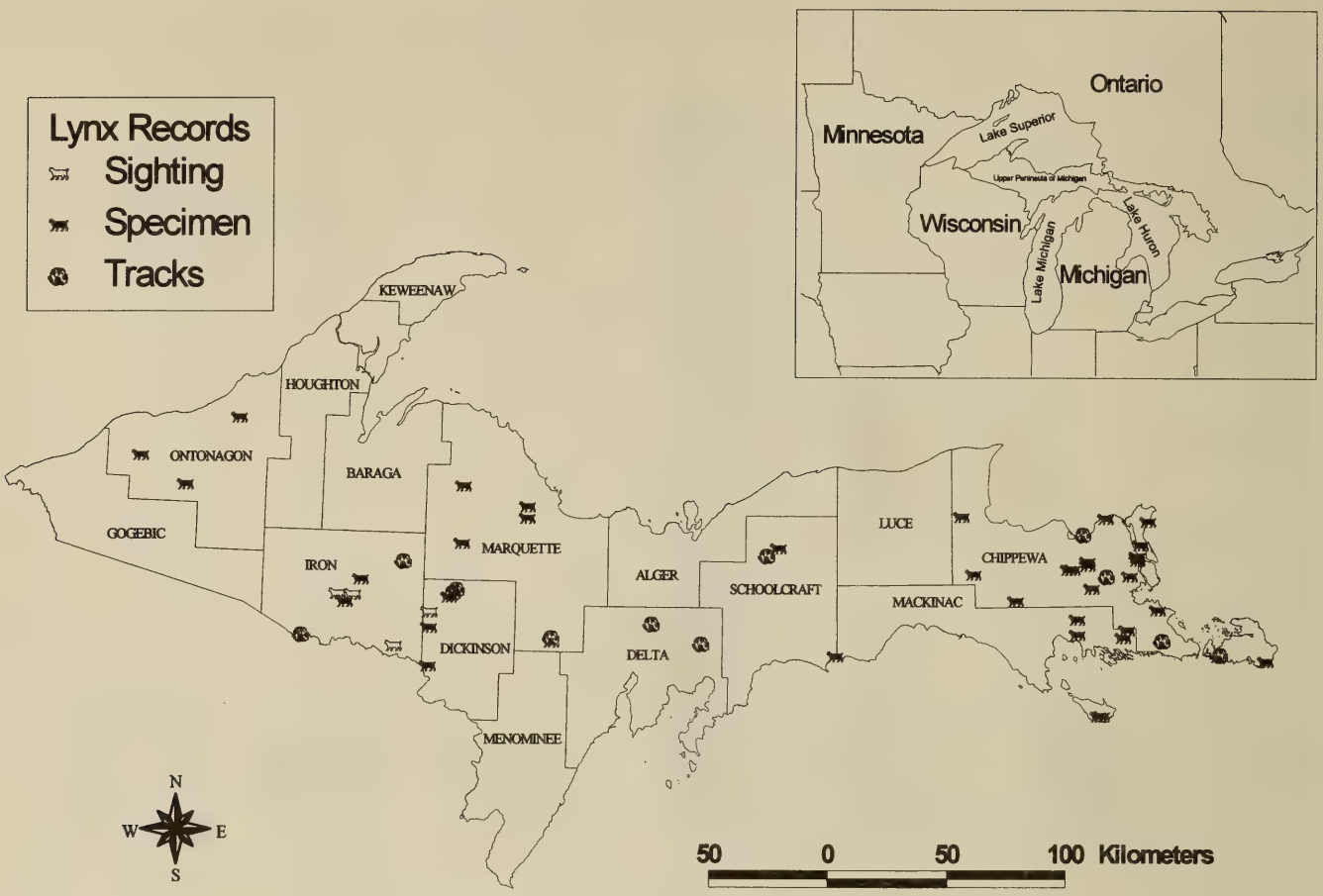

FIGURE 2. Type and distribution of spatially referenced Canada Lynx occurrence records in the Upper Peninsula of Michigan, 1940–1997.

Track Surveys

The wolf track count survey was initiated in 1992, however, coverage was primarily limited to the western Upper Peninsula during the first two years. Coverage across the Upper Peninsula began in 1994 and has been relatively consistent since then. The most complete documentation for the extent of this survey is from 1999. Observers spent approximately 1500 person hours searching 8555 km (Figure 3) of roads and trails for wolf and other predator sign. Effort was similar during 1994–1998. No lynx tracks have ever been found in the wolf track count efforts.

The furbearer track count survey was initiated in 1997 when 163 km of roads and trails were searched. In 1998, survey effort more than doubled with 402 km of roads and trails searched (Figure 3). No lynx tracks were found on the furbearer track count routes in 1997 or 1998.

Residency Status

Verified records show that lynx have been present, at least periodically, in the Upper Peninsula during the period of 1940–1997. Extensive track count efforts, results of mandatory check of Bobcats, and the paucity of recent records indicate that lynx are currently absent or very rare in the Upper Peninsula. However, an important question is whether or not a small resident population of Canada Lynx exists. The U. S. Fish and Wildlife Service (1998) defines a resident population as "a group or subgroup of lynx in an area or portion of a larger area that is capable of long-term persistence, based on self-sustaining reproduction of young and successful recruitment of young into the breeding age cohort, without immigration of lynx from Canada." Thus, the two important elements of a resident population are long-term persistence and successful reproduction. It is very difficult to prove unequivocally that a small remnant population does not exist, especially in an area the size of the Upper Peninsula of Michigan. Thus, we can only present circumstantial evidence.

We found no verifiable evidence of successful reproduction within the Upper Peninsula of Michigan. The last unverified record of Canada Lynx kittens is over 20 years old and there were only two unverified records since 1940. A tremendous amount of effort has been expended on track surveys since 1994, yet no lynx sign has been located. While the records indicate that a few individuals may have been present but not detected by these surveys, it seems unlikely that an entire population of lynx would have been missed. The mean home range size for male lynx in the southern boreal forests is 151 km^2 (Aubry et al. 1999), larger than any wilderness area in the

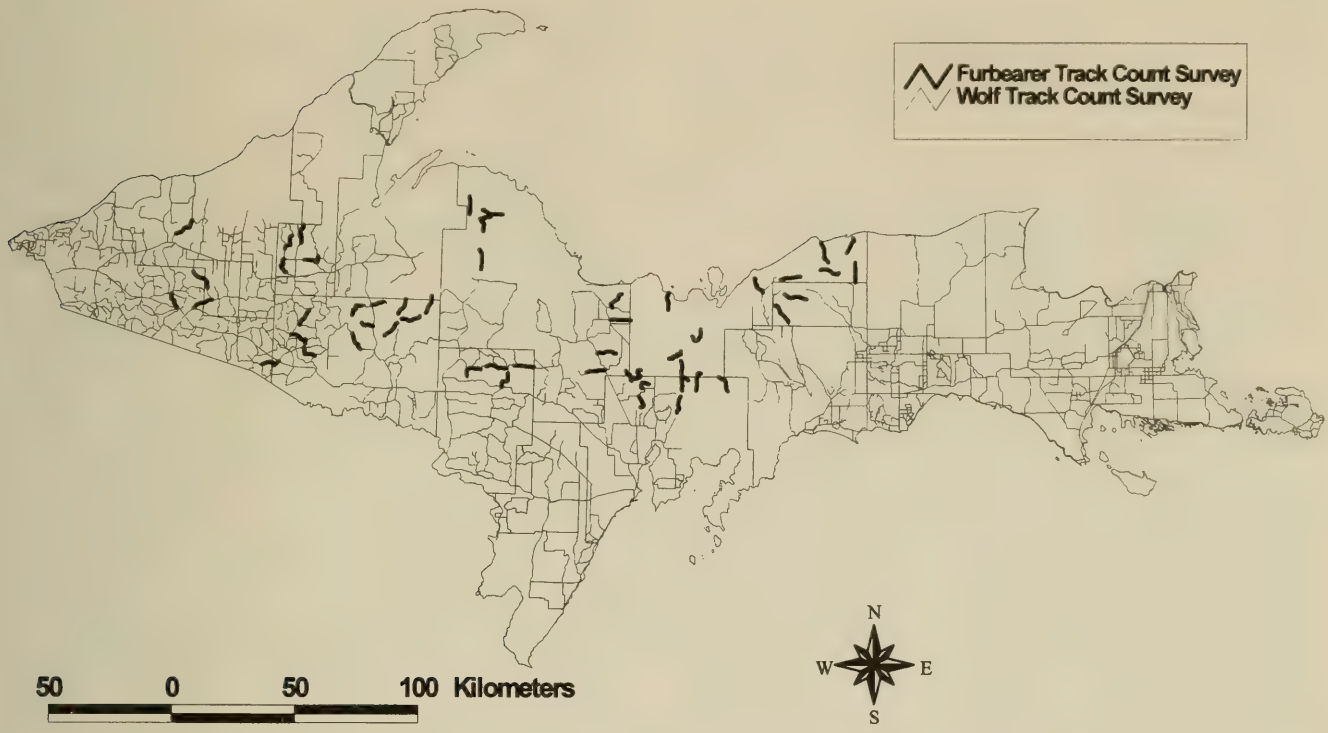

FIGURE 3. Map of Michigan's Upper Peninsula showing roads and trails surveyed for Gray Wolves in 1999 and furbearers in 1998. No Canada Lynx tracks were observed in wolf surveys (1994–1999) or furbearer surveys (1997–1998).

Upper Peninsula. This suggests it is very unlikely for an individual lynx, let alone a population, to completely occur in an area that receives low human visitation. In addition to formal surveys, natural resource professionals, hunters, trappers, and other recreationists spend a considerable amount of time in all areas of the Upper Peninsula. This results in observations of other rare predators. For example, a substantial number of citizen observations of Gray Wolves (> 50) were reported even when the wolf population numbered fewer than 25 animals (Michigan Department of Natural Resources, unpublished data). Except for the 1960s, there were six or fewer observations of lynx occurrence per decade. The increase in occurrences in the 1960s was associated with an unusually large population irruption in Canada (Theil 1987; McKelvey et al. 1999a).

McKelvey et al. (1999a), like Theil (1987), concluded that recent lynx dynamics in the Great Lakes States appears to be related to immigration from Canada. In addition, McKelvey et al. (1999a) looked for a lynx population response to large increases in Snowshoe Hare populations throughout the Great Lakes Region. They reasoned that a resident population should have responded to the periodic increases in the number of hares. No association between lynx occurrence data and Snowshoe Hare population indices was found. Similarly, there is no association between lynx occurrences and a Snowshoe Hare population index in the Upper Peninsula (Michigan Department of Natural Resources, unpublished data). While McKelvey et al. (1999a) are correct in pointing out that these data do not prove whether or not a local population exists, they certainly do not provide support for the existence of a resident population.

In conclusion, we found no evidence to suggest that a resident lynx population might exist in Michigan's Upper Peninsula. The evidence suggests that lynx dispersing from Canada are only occasionally present in the Upper Peninsula. Although the dynamics of lynx colonization are unknown, McKelvey et al. (1999b) provide a good theoretical discussion of the dynamics and probabilities of successful colonization.

Acknowledgments

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Diet of the Prairie Rattlesnake, *Crotalus viridis viridis*, in Southeastern Alberta

MARGARET M. A. HILL, G. LAWRENCE POWELL, and ANTHONY P. RUSSELL

Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada

Hill, Margaret M. A., G. Lawrence Powell, and Anthony P. Russell. 2001. Diet of the Prairie Rattlesnake, *Crotalus viridis viridis*, in southeastern Alberta. Canadian Field-Naturalist 115(2): 241–246.

The diet of the Prairie Rattlesnake, *Crotalus viridis viridis*, in a multiple land use area in southeastern Alberta was investigated by examining the gut contents of 20 road-killed individuals and the composition of eight scats recovered from sequestered individuals. All individuals yielding dietary data were adults. No data on the composition of the local small mammal community are available. The number of prey items per snake varied (gut contents: 0–4 items; scat samples: 1–3 items). Frequency of occurrence (individual prey items) was: Sagebrush Vole (*Lagurus curtatus*) — 53% gut contents, 68% scats; Meadow Vole (*Microtus pennsylvanicus*) — 38% gut contents, 8% scats; Olive-Backed Pocket Mouse (*Perognathus maniculatus*) — 8% scats; Western Jumping Mouse (*Zapus princeps*) — 8% scats; Richardson's Ground Squirrel (*Spermophilus richardsonii*) — 8% scats; unidentified passerines — 9% gut contents. Although individual rattlesnakes sometimes took more than one prey taxon (gut contents: 1–3 taxa; scat samples: 1–2 taxa), multiple prey items in a single gut were almost always of the same species, suggesting that individual rattlesnakes tend to exploit patches where colonial burrowing prey species are abundant.

Key Words: Prairie Rattlesnake, *Crotalus viridis viridis*, diet, gut contents, scats, Alberta.

The Prairie Rattlesnake (*Crotalus viridis viridis*) reaches its northernmost geographical range limit in southeastern and central Alberta and southwestern Saskatchewan (Pendlebury 1977; Gannon and Secoy 1984, 1985; Russell and Bauer 2000). Various aspects of its ecology in this part of its range have been described (Lewin 1963; Pendlebury 1977; Gannon 1978; Macartney and Weichel 1993; Gannon and Secoy 1984, 1985; Kissner et al. 1996*), but its diet in this portion of its range has received relatively little attention (Gannon and Secoy 1984). Here we describe observations on the diet of adult *C. v. viridis* from a population in southeastern Alberta. The data were derived from necropsies of dead adult specimens recovered from a road that crossed our study area, and from analysis of scats from sequestered wild-caught rattlesnakes, in the course of a radiotelemetric study of movement and habitat use in this population.

Materials and Methods

Study Site

The study area (approximately 9000 ha in extent, centred on 50°10'30"N, 110°30'W; W4M, 14, 4–5) is located in an area of mixed range and cropland roughly 20 km NW of the city of Medicine Hat, Alberta. It is rolling, with large coulees running to the east from the South Saskatchewan River's channel, and much of the area supports the mixed grass prairie association (Coupland 1950; Strong 1992*), modified by the grazing of domestic cattle. Human uses of the study area include cattle ranching, grain and hay cultivation, hunting, and natural gas exploration and extraction. Prairie Rattlesnakes are well-known from this area (Pendlebury 1977; Watson and Russell 1997). There is a diverse potential prey pool of small mammal species (Soper 1964; Smith 1993) and ground-nesting grassland passerines (Semenchuk 1992) available in the area.

Dietary analysis

For dead-on-the-road (DOR) rattlesnakes, date of collection, snout-vent length (SVL) and weight (when the state of the carcass permitted), location and sex of each individual were recorded prior to fixation in 10% neutral buffered formalin (as soon as possible after discovery) and subsequent preservation in 70% ethanol. Wild-caught adult rattlesnakes from the study area were also held in the laboratory, either for radio-transmitter implantation or specifically for scat collection, and their scats retained. Date and capture location of the donor were recorded for scats.

Each DOR snake was radiographed and the positions of gut contents (oesophagus, stomach, small intestine, and large intestine [including cloaca]) were recorded before they were removed from the body by dissection. Diagnostic bones or bone fragments (e.g., mandibles, femora, humeri etc.) were isolated, identified and counted in order to determine the minimum number of identifiable mammalian prey items per species per snake. Samples of hair were also taken from each gut section and kept for identification purposes. Identification of mammalian prey items to species was made by comparing skulls and tooth cusp patterns of identified reference specimens (from the

*See Documents Cited section

University of Calgary Museum of Zoology) to those found in the gut, and by features of the external hair surface such as overall shape and cuticular scale pattern.

Scats were softened in tap water for about 20 minutes and then teased apart under a dissecting microscope using watchmaker's forceps. All diagnostic bone fragments, and hair samples, were recovered and retained from each as described for the gut contents above.

Due to the small size of the sample as a whole, differences in diet between the sexes were not tested, nor were differences between size classes, as there was little variation in SVL among the DOR snakes. The relationship between the number of prey items and the number of prey taxa in rattlesnake guts was tested by a Pearson's correlation coefficient. The incidences of the main prey species in rattlesnake guts were tested for independence of occurrence by a G-test (Sokal and Rohlf 1995). Temporal patterns in the distributions of the main prey species through the study period are examined graphically; patterns of incidences and numbers of captures are compared with Sign tests, Wilcoxon Signed-ranks tests and Wald-Wolfowitz Runs tests, carried out with SYSTAT (Wilkinson 1990). The statistical analysis of the gut data was intended to detect patterns of prey encounter. *Crotalus v. viridis* has elsewhere been shown to exploit patches of high prey density (Duvall et al. 1985, 1990), and a number of the potential prey species in this area occupy localized burrow systems (Soper 1964; Pattie and Hoffmann 1992*; Nietfeld and Roy 1993*). The data from the scat sample are treated separately from the gut sample and are not analysed statistically; we have no data on how long faeces are retained in free-ranging rattlesnakes and cannot assume that an individual scat represents the remnants of a single feeding bout.

Results

Material Examined

Twenty freshly-killed DOR snakes were collected during the 1997 field season (1 May–15 October) along RR 43 (5 females, 15 males — all DOR specimens were sexually mature). Eight scats were collected from wild-caught adult individuals temporarily held in the lab.

Diet composition

A total of 32 prey items (three avian, 29 mammalian) were recovered from the 20 DOR individuals (Table 1). In all three cases of avian remains, mammalian hair and bone fragments were found in the same region of the gut, intermixed with feathers. Mammalian remains only, representing 13 individual prey items, were retrieved from the 8 scats (Table 1).

A few individual snakes had gut or scat contents at the upper range of dietary diversity, but snakes taking single prey taxa frequently took several items (Tables 2, 3). The modal number of items in the gut was 1 (range 0–4), and the modal number of taxa was 1 (range 0–3). For scats, the modal number of items was 1 (range 1–3) and the modal number of taxa 1 (range 1–2). There was a positive high correlation between the number of items and the number of prey taxa in the gut (Table 2); the pattern is less clear-cut in the scats (Table 3). When the numbers of *Microtus pennsylvanicus* and *Lagurus curtatus* (the two commonest prey species: Table 1) in guts were cross tabulated a pattern was evident; of the 17 guts containing these two species, they co-occurred only in three, in each case represented by one individual of each prey species, and the distributions of the numbers of each species were independent (Table 4); snakes tended to feed upon one or the other. Only one scat contained *M. pennsylvanicus* remains, and it contained no *L. curtatus* remains (Table 5). The distributions of neither *L. curtatus* nor *M. pennsylvanicus* in guts are significantly clustered in time through the study period (Figure 1; Wald-Wolfowitz Runs test: *L. curtatus* $Z = -0.429$; $p = 0.668$; *M. pennsylvanicus* $Z = -1.097$; $p = 0.272$). The temporal distributions of the two prey species in guts broadly overlap over the study period (Figure 1) and there are no significant differences in either the number of days over the study period in which rattlesnakes preyed on either *L. curtatus* or *M. pennsylvanicus* (Sign test;

TABLE 1. Prey of adult Prairie Rattlesnakes (*Crotalus viridis viridis*) north of Medicine Hat, Alberta, from gut contents of road-killed snakes (20 individuals) and scats (8 individuals). See text for methods of prey species identification.

	Gut Contents		Scats	
Prey Species	No. of Prey Items	% of Total	No. of Prey items	% of Total
Lagurus curtatus (Sagebrush Vole)	17	53.12	9	69.23
Microtus pennsylvanicus (Meadow Vole)	12	37.50	1	7.69
Perognathus maniculatus (Olive-Backed Pocket Mouse)	0	0.00	1	7.69
Zapus princeps (Western Jumping Mouse)	0	0.00	1	7.69
Spermophilus richardsonii (Richardson's Ground Squirrel)	0	0.00	1	7.69
Unidentified Passerine Birds	3	9.38	0	0.00
Totals	32		13	

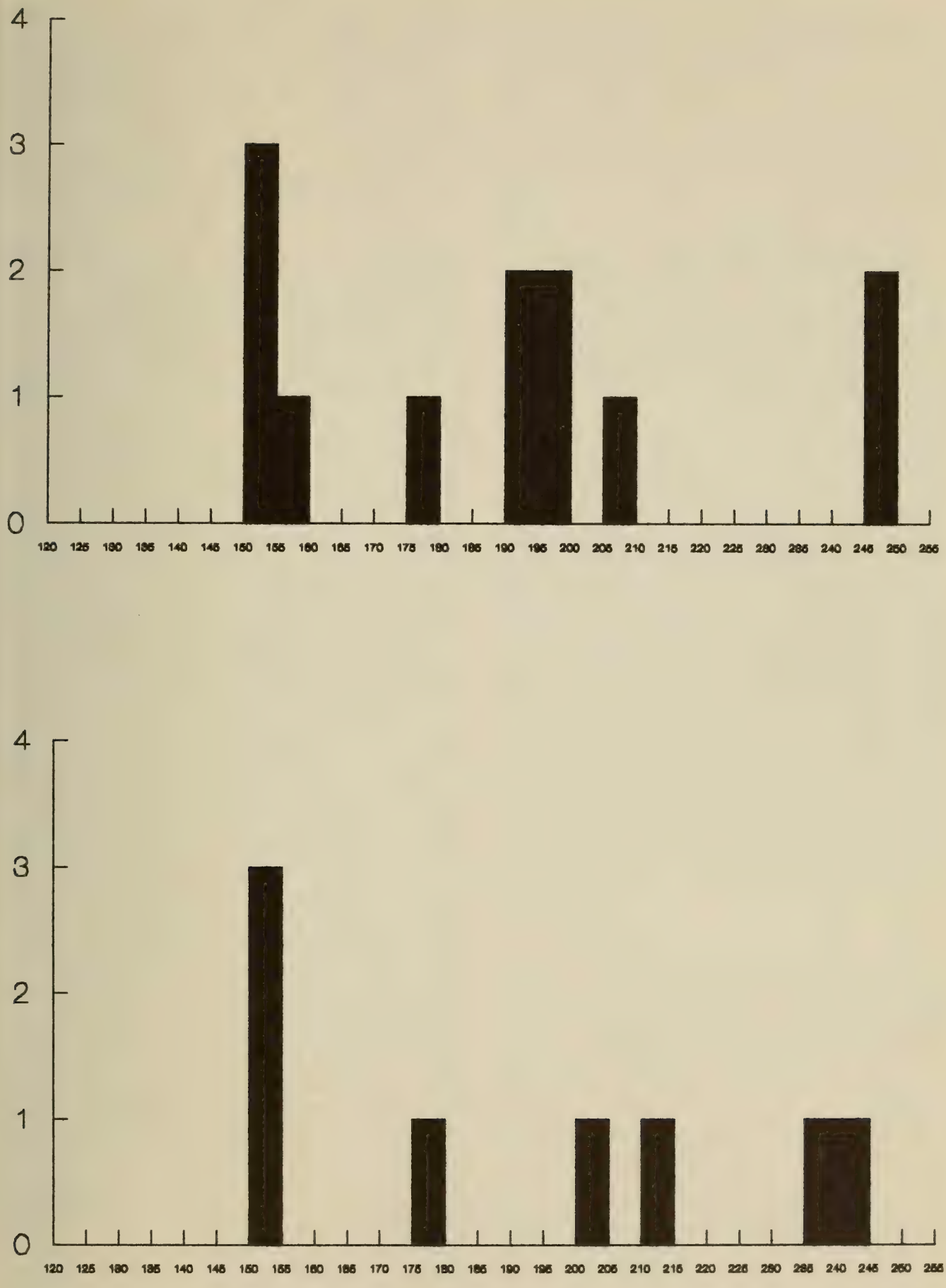

FIGURE 1. Distributions of (above) the number of *Crotalus viridis viridis* with *Lagurus curtatus* in their guts over the study period; n = 12; and (below) the number of *Crotalus viridis viridis* with *Microtus pennsylvanicus* in their guts over the study period; n = 8. The verticle axis gives the number of rattlesnakes and the horizontal the Julian day in 1997 (counting day 1 as 1 January).

TABLE 2. Cross-tabulation of number of prey items per gut and number of prey taxa per gut for twenty DOR *Crotalus viridis viridis* from study area (– = not applicable). Pearson's r = 0.722, p < 0.001.

	No Prey	One Item	Two Items	Three Items	Four Items
Three Taxa	–	–	–	1	0
Two Taxa	–	–	3	0	1
One Taxon	–	7	3	2	0
No Prey	3	–	–	–	–

p = 0.494), or in the number of prey of either species that a rattlesnake was likely to be carrying in its gut (Wilcoxon Signed-ranks test; Z = -0.835; p = 0.404). Within gut samples, items were much more abundant in the stomach and small intestine than in the large intestine, particularly multiple occurrences of *L. curtatus* and *M. pennsylvanicus*.

Discussion

All of the DOR snakes were collected along RR 43, a transect that runs directly through the activity ranges of at least part of the area's summer rattlesnake population. The disturbed soil of the ditches flanking the roadbed may have represented a particularly favourable microhabitat for burrowing rodents and thus attracted a disproportionate number of rattlesnakes compared to the surrounding relatively undisturbed prairie. If this is the case our sample is biased, representing rattlesnakes preying upon rodent species that dwelt preferentially on disturbed ground. Without data on rodent distribution among microhabitat types in this area, this possibility cannot be assessed.

Only five of 20 DORs were female, which may be a function of the small sample size rather than a sampling bias. However, reproduction appears to be biennial for female *Crotalus v. viridis* at this latitude (Gannon and Secoy 1984; Macartney and Weichel 1993; Kissner et al. 1996*), in which case we would expect a male:female ratio of approximately 13:7 in the wide-ranging fraction of the adult population, if all of the gravid females remained close to the hibernacula (Gannon and Secoy 1984) and if the natal sex ratio is 1:1. This ratio is close to what we found and none of the DOR females were carrying developed embryos.

Crotalus viridis is a very widely distributed species (Klauber 1972), and shows considerable variety in its diet over its range. In the more southerly portions, larger *C. viridis* have been observed to take subadults of any species of ground squirrel (*Spermophilus*) locally present, as well as subadult Black-tailed Prairie Dogs (*Cynomys ludovicianus*) and Nuttall's Cottontail (*Sylvilagus nuttallii*); species of *Dipodomys, Neotoma, Perognathus, Reithrodontomys, Peromyscus*, and *Microtus* are also taken (Fitch and Twining 1946; Fitch 1949; Klauber 1972; Ludlow 1981; Duvall et al. 1985, 1990; Diller and Johnson 1988; Macartney 1989; Wallace and Diller 1990; Diller and Wallace 1996). Also, Lark Buntings (*Calamospiza*) and other ground-nesting bird species have been recorded as frequent prey; lizards and frogs are taken predominantly by subadult snakes (Klauber 1972). Duvall et al. (1985, 1990) showed that the annual movement patterns of the seasonally migratory adults in a high-elevation population of *Crotalus v. viridis* in southern Wyoming were strongly associated with the distribution across the landscape of local concentrations of *Peromyscus maniculatus*, which constituted the rattlesnake's principal prey in this area.

We found *Crotalus v. viridis* in this part of southeastern Alberta to subsist primarily on *Lagurus curtatus* and *Microtus pennsylvanicus*, and to a much smaller extent upon three other terrestrial rodent species and an unknown passerine (Table 1). Results

TABLE 3. Cross-tabulation of number of prey items per scat and number of prey taxa per scat for eight *Crotalus viridis viridis* scats from study area (– = not applicable).

	One Item	Two Items	Three Items
Two Taxa	–	2	0
One Taxon	4	1	1

TABLE 4. Cross-tabulation of number of individual *Lagurus curtatus* per gut and number of individual *Microtus pennsylvanicus* per gut for twenty DOR *Crotalus viridis viridis* from study area. G = 9.17, 9 df; NS.

	No *Lagurus*	One *Lagurus*	Two *Lagurus*	Three *Lagurus*
No *Microtus*	2	5	3	1
One *Microtus*	3	3	0	0
Two *Microtus*	0	0	0	0
Three *Microtus*	2	0	0	0

TABLE 5. Cross-tabulation of number of individual *Lagurus curtatus* per scat and number of individual *Microtus pennsylvanicus* per scat for eight *Crotalus viridis viridis* scats from study area.

	No *Lagurus*	One *Lagurus*	Two *Lagurus*	Three *Lagurus*
No *Microtus*	1	4	1	1
One *Microtus*	1	0	0	0

of this study agree with observations in previous literature, in that the diet consists primarily of small mammals (Klauber 1972; Mushinsky 1987). The relative abundances of the prey species taken by our sample of adult Alberta *C. viridis*, in addition to the absence of Pocket Gophers (*Thomomys bottae*) and White-footed Mice (*Peromyscus maniculatus*), and the rarity of Richardson's Ground Squirrels (*Spermophilus richardsonii*) in guts or scat (Table 1), are difficult to evaluate, since there are no quantitative data on the composition of the local small mammal community. The absence of *P. maniculatus* is particularly puzzling, as this species is generally abundant on the Alberta mixed-grass prairies (Soper 1964; Pattie and Hoffmann 1992*; Smith 1993) and is an important prey species for *C. viridis* elsewhere (Duvall et al. 1985, 1990; Macartney 1989). *Spermophilus richardsonii*, a visible species when present, was seldom seen in the study area during the summer of 1997, suggesting that local population densities were low. Both *P. maniculatus* and *S. richardsonii* were found in *C. viridis* guts in the vicinity of Leader, Saskatchewan, by Gannon and Secoy (1984), indicating that they are both dietary items in this part of its range. Of the prey species that did occur in our sample, both *L. curtatus* and *Perognathus fasciatus* are considered to be rare in Alberta (Smith 1993), although the former can apparently attain localized high densities (Soper 1931; Pattie and Hoffmann 1992*). Both *Microtus pennsylvanicus* and *Lagurus curtatus* form colonies marked by burrow and runway construction (Soper 1931, 1964; Pattie and Hoffmann 1992*), whereas *Perognathus fasciatus* and *Zapus princeps* are solitary burrowers (Soper 1964; Pattie and Hoffmann 1992*). *Crotalus viridis*, an ambush predator (Klauber 1972; Diller and Wallace 1996), favours waiting in burrows for rodents to enter them (Duvall et al. 1985, 1990), and all of these species would be vulnerable to such tactics.

The relationship between the number of prey items and number of prey taxa per rattlesnake (Tables 2, 3) suggests that individual rattlesnakes in this area exploit patchily distributed rodent colonies. Most gut (Table 2) and scat (Table 3) samples yielded prey items of only one taxon, regardless of their number. This would be expected in a predator exploiting a patch of high prey density. The frequency of rattlesnakes that had consumed more than one prey item (Tables 2, 3) also suggests exploitation of a patchily distributed resource, as does the tendency of multiple prey items in single guts to be restricted to the stomach and small intestine. Macartney (1989) seldom found more than one prey item or one prey taxon per snake in his study of an Okanagan Valley population of *Crotalus v. oreganus*, which did not display the movement patterns, apparently associated with prey distribution, typical of our population (Russell et al. unpublished data) or that studied by Duvall et al. (1985, 1990). The relationship between the presence of *M. pennsylvanicus* and that of *L. curtatus* (Tables 4, 5; Figure 1) in guts and scats is further evidence that runway systems of either colonial species were a particular target of the rattlesnakes in our sample, and that they tended to catch large numbers of prey individuals in such systems. The lack of difference in the temporal distributions of these two prey species (Figure 1) in DOR rattlesnakes suggests further that high prey density was the criterion for patch choice, rather than prey species.

Avian remains in *C. viridis* gut contents have been reported from other studies (Fitch 1949; Klauber 1972; Wallace and Diller 1990). Those found in our sample are most likely the fledglings of one of a number of ground-nesting species of passerine, the adults of which are known to frequently leave the immediate area of the nest, possibly in response to the threat of nest predation (Dorothy Hill, personal communication). It is probable that this occasional consumption of fledgling birds is opportunistic, because it is so rarely observed, and because, in the case of this study, avian remains were always found in association with mammalian remains in the gut.

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Effects of Enclosed Large Ungulates on Small Mammals at Land Between The Lakes, Kentucky

Clare C. Weickert, Joseph C. Whittaker, and George A. Feldhamer

Department of Zoology, Southern Illinois University at Carbondale, Carbondale, Illinois 62901 USA

Weickert, Clare C., Joseph C. Whittaker, and George A. Feldhamer. 2001. Effects of enclosed large ungulates on small mammals at Land Between The Lakes, Kentucky. Canadian Field-Naturalist 115(2): 247–250.

Ungulates can affect primary production, plant and animal species composition, nutrient cycling, and soil properties. We conducted a study at the Tennessee Valley Authority's Land Between The Lakes to investigate the effects of introduced Elk (*Cervus elaphus*) and Bison (*Bison bison*) on small mammal fauna in a 324-ha enclosure. From June 1998 through May 1999, live traps were set for small mammals in open-canopy hardwood, closed-canopy hardwood, and pine sites both inside and outside the enclosure, for 7020 trap nights. Small mammals were captured significantly more often inside than outside the enclosure; habitat type was not a significant factor. Habitat management practices inside the ungulate enclosure, including burning, mowing, and fertilizing, may have contributed to the higher abundance of small mammals.

Key Words: Bison, *Bison bison*, Elk, *Cervus elaphus*, Land Between The Lakes, Kentucky, small mammals, ungulates

Small mammal populations provide a critical resource base for a variety of wildlife species at higher trophic levels. Ungulates can affect sympatric small mammal populations both directly and indirectly. Ungulates may reduce forage available for herbivorous small mammals by consuming vegetation and mast, or by altering local plant species composition (Horsley and Marquis 1983; Augustine and McNaughton 1998). Reduction or prevention of tree and shrub regeneration as a result of ungulate browsing in forest habitats (Crouch 1981; Putman 1986; Gill 1992) may result in long-term changes in canopy species composition and structure (Healy 1997; Singer et al. 1998). Feeding, trampling, and wallowing by ungulates also reduces protective vegetation cover, potentially increasing vulnerability of small mammals to predation (Grant et al. 1982; Bock et al. 1984). Small mammal populations also may be influenced positively by ungulates. Ungulate defecation can contribute to accelerated nutrient cycling (McNaughton 1985) and seed dispersal (Janzen 1986; Malo and Suarez 1995). Also, antlers shed by cervids provide supplementary dietary minerals for small mammals that consume them (Couturier 1995). Generally, however, cumulative abundance of small mammals is greater on areas from which ungulates are excluded (Bock et al. 1984; Heske and Campbell 1991; Hayward et al. 1997; Keesing 1998).

Most previous studies on the effects of ungulates on small mammals have been conducted in desert or semi-desert habitats. An introduction of Elk (*Cervus elaphus*) and Bison (*Bison bison*) to a large enclosure provided an opportunity to examine the ecological impact of high ungulate density on relative abundance of small mammals in deciduous and pine forested habitats.

Methods and Materials

Our study was conducted in the Trigg County, Kentucky, portion of Land Between The Lakes (LBL), an approximately 70 000-ha natural area administered during the period of the study by the Tennessee Valley Authority in western Kentucky and Tennessee. LBL extends from approximately 36°30′ to 37°00′N, 87°50′ to 88°05′W (see Burbank and Smith [1966] for a description of habitat and hydrology of LBL). In January 1996, 29 wild Elk from Alberta, Canada, were released into a newly constructed, 324-ha drive-through wildlife viewing area enclosed with a 3-m-high deer-proof fence. During summer 1996, 44 Bison from an existing LBL herd were released into the enclosure. White-tailed Deer (*Odocoileus virginianus*) occurred naturally both inside and outside the enclosure. During the study, total ungulate density inside the enclosure, including Elk, Bison, and White-tailed Deer, was approximately 46.2 /km^2. Elsewhere on LBL, the estimated density of White-tailed Deer was between 6.2 and 10.0 deer/km^2 (S. Bloemer, LBL, unpublished census data). There were no free-ranging Elk or Bison outside the enclosure.

We sampled 12 forested sites for small mammal abundance during this study: six inside the enclosure (experimental) and six that were ≤10 km from the enclosure (control sites). Each group of six sites included two open-canopy hardwood sites (this habitat type comprised approximately 5.0% of the enclosure), two closed-canopy hardwood sites (this habitat type comprised approximately 40.8% of the enclosure), and two pine sites (this habitat type comprised approximately 4.8% of the enclosure). Hardwood sites were dominated by an overstory of Oak (*Quercus* spp.) and Hickory (*Carya* spp.). Common understory was Oak, Hickory, Persimmon (*Diospyros virgini-*

ana), Black Cherry (*Prunus serotina*), and Sassafras (*Sassafras albidum*). Pine sites were dominated by an overstory of Virginia Pine (*Pinus virginiana*), with a sparse understory of Oak and Ash (*Fraxinus* sp.). Stand age, most recent harvest date, and gross vegetation structure (mean DBH, canopy closure, fallen logs) were similar for sites inside and outside the enclosure. In the enclosure, some forested area was cleared and planted to warm- and cool-season grasses, primarily Indiangrass (*Sorghastrum nutans*), Little Bluestem (*Andropogon scoparium*), and Switchgrass (*Panicum virgatum*), as well as Bush Clover (*Lespedeza* sp.). Grasslands, including recently cleared and originally existing areas, made up the remainder of the enclosure. We did not trap small mammals on grassland areas, however, because there were no grassland sites outside the enclosure for controls. Elk and Bison used all habitat types within the enclosure based on deposition of fecal material (Weickert, unpublished data). Within the enclosure, forested areas were burned on an irregular schedule, and grassland patches were burned, fertilized, and mowed on an irregular schedule of approximately 12 months. Ungulates were supplementally fed with hay and, periodically, commercially produced pelletized feed during winter months.

A 100-m transect with 10-m spacing between trap stations was set at each site. Fifteen small (5.1 × 6.4 × 16.5 cm) Sherman live traps (H. B. Sherman Co., Tallahassee, Florida) baited with cracked corn and sunflower seeds were used on each transect, with one or two traps at alternate stations. We sampled each site 13 times (at about four- to five-week intervals), for three nights each time, during the period from June 1998 through May 1999. Experimental and control sites were sampled simultaneously to alleviate influences such as weather or moonlight. Trapping effort totaled 585 trap nights per site, and a total of 7020 trap nights. We toe-clipped captured mammals and recorded their body mass, sex, and reproductive condition. Animals were released at the point of capture. Data on small mammal captures were transformed ($\log_{10}$). Data were analyzed using two-way analysis of variance with enclosure and habitat type as factors. Analyses were considered significant at $P < 0.05$.

Results

We captured a total of 145 individuals of five species of small mammals inside the ungulate enclosure, compared to 96 individuals of three species on the control sites (Table 1). White-footed Mice (*Peromyscus leucopus*) comprised 89.7% of the individuals inside the enclosure and 71.9% of individuals outside the enclosure. Across all habitat types, there were more total small mammal captures (initial captures and recaptures) inside the enclosure than outside ($F = 11.27$, $P = 0.015$). Habitat type was not a significant factor ($F = 4.07$, $P = 0.076$) nor was the interaction between habitat type and enclosure type ($F = 2.55$, $P = 0.156$).

Discussion

The greater abundance of small mammals captured inside the high-ungulate-density enclosure was unexpected. Similar studies, as noted, have generally shown lower abundance of small mammals in areas of high ungulate density. Keesing (1998), working in East African savanna habitat, found that the African Pouched Rat (*Saccostomus mearnsi*), the most common small mammal species in the area, responded to the exclusion of ungulates by increasing two-fold in density within one year (40% higher abundance than outside the exclosures). Similarly, Bock et al. (1984) and Heske and Campbell (1991) captured cumulatively more rodents inside areas from which livestock and Mule Deer (*Odocoileus hemionus*) had been excluded in Arizona. Hazebroek et al. (1995) captured significantly more small mammals inside than outside areas in hardwood and pine stands in the central Netherlands from which Red Deer (*Cervus elaphus*), Roe Deer (*Capreolus capreolus*), and Wild Boar (*Sus scrofa*) had been excluded for the six years prior to their study.

Unfortunately, we could not determine the relative abundance of small mammals in the enclosure prior

TABLE 1. Species and number of individual small mammals captured from June 1998 through May 1999 on three habitat types (P = pine forest; CC = closed-canopy forest; OC = open-canopy forest) inside and outside of an ungulate enclosure on Land Between The Lakes, Kentucky.

	Inside Enclosure			Outside Enclosure		
Species	P	CC	OC	P	CC	OC
Peromyscus leucopus	48	46	36	20	19	30
Blarina brevicauda	2	1	5	16	5	1
Microtus pinetorum	0	1	1	0	1	4
Ochrotomys nuttalli	0	0	4	0	0	0
Glaucomys volans	0	1	0	0	0	0
Totals	50	49	46	36	25	35

to the introduction of Elk and Bison. The site of the enclosure was chosen primarily because it was centrally located on LBL and contained a small, remnant portion of native prairie. There were no pre-existing differences known in any of the forest habitats that would have caused greater abundance of small mammals to occur prior to enclosure. Therefore, we expect that small mammal abundance was initially the same as on control sites.

Several factors may have affected our results. The ungulate viewing enclosure on LBL was two years old at the start of the study. The resident ungulates may not yet have altered the forest habitats to the point of depleting food resources or protective herbaceous cover for sympatric small mammals. The approximately 5× higher ungulate density inside the enclosure than outside has led to a proportionally higher rate of dung deposition. This may be benefiting the small mammals by allowing more rapid nutrient cycling through the system. Janzen (1986) found that some rodents mined and consumed seeds from ungulate dung. In North America, mice, specifically *Peromyscus* sp., and other small mammals are known to mine and consume seeds from the dung of bears (*Ursus* sp.; Bermejo et al. 1998) and Raccoons (*Procyon lotor*; Page et al. 1999). If they are also consuming seeds from ungulate dung, the dung inside the high-ungulate-density enclosure may provide an additional food source. Herbivorous or generalist small mammals may consume vegetation newly sprouted from those seeds. Also, insectivores and generalists may feed upon the accompanying invertebrate resource. The Elk and Bison dung probably contains fewer seeds, however, than that of omnivorous bears and Raccoons.

Aside from the high ungulate density, factors most strongly affecting the habitat inside the enclosure were the management activities designed to maximize quality and quantity of forage for the ungulates — burning, fertilizing, and supplemental feeding. Burning and fertilizing may directly influence small mammals by promoting new forage available to them. Indirect benefits may result from supplemental hay by increasing available forage for ungulates and reducing their effects on the vegetation.

Based on the results of previous studies, small mammal populations within the enclosure may decline if the high-density ungulate populations are permitted to effect more drastic changes in their habitat than have thus far been observed. Currently, however, the expected negative impact of high ungulate density on the cumulative abundance of small mammals appears to have been outweighed by habitat management practices that promoted small mammal abundance. Introduction of free-ranging ungulates probably will not include these habitat management practices, and more "typical" negative effects on small mammal populations might be expected.

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Thermal Habitat Use and Evidence of Seasonal Migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana

SUSAN B. ADAMS[1] and CHRISTOPHER A. FRISSELL[2]

Flathead Lake Biological Station, The University of Montana, Polson, Montana 59860 USA
[1]Present address and correspondence to: USDA Forest Service, Southern Research Station, 1000 Front Street, Oxford, Mississippi 38655 USA
[2]Present address: The Pacific Rivers Council, PMB 219, 1 Second Avenue E., Suite C, Polson, Montana 59860 USA

Adams, Susan B., and Christopher A. Frissell. 2001. Thermal habitat use and evidence of seasonal migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana. Canadian Field-Naturalist 115(2): 251–256.

All life stages of Rocky Mountain Tailed Frogs (*Ascaphus montanus*) occurred in a reach of Moore Creek, Montana, where water temperatures exceeded those previously reported for *Ascaphus* in the wild. However, relative density of *Ascaphus* in the warmest reach, immediately downstream of a lake outlet, was lower than in cooler reaches downstream. Although we observed larvae and frogs in water temperatures up to 21°C, cold groundwater seeps contributed to a spatially complex thermal structure in the warmest stream reach. Frogs congregating near a cold seep and nesting in a groundwater-influenced site were likely using behavioral thermoregulation. At a stream weir in the warmest reach, we captured 32 Tailed Frogs moving downstream and none upstream, in September and October 1997. Because no migration was evident at five other weirs where summer water temperatures remained below 16°C, we propose that the frogs moving through upper Moore Creek migrated seasonally to avoid the high temperatures. The mature frogs may spend summers in the small, cold lake inlet streams, moving downstream in the fall to overwinter. Behavioral studies would be necessary to determine the extent to which individuals limit their overall thermal exposure in such spatially complex environments. Migration in response to local, seasonally changing habitat suitability could explain the diverse, and apparently contradictory, movement patterns (or lack thereof) among *Ascaphus* populations reported in the literature. Future studies of *Ascaphus* movements could benefit by accounting for seasonal changes in habitat suitability and by quantifying in-stream movements.

Key Words: *Ascaphus montanus*, Tailed Frog, amphibian, water temperature, thermal complexity, habitat, movements, migration, behavior.

Tailed Frogs (*Ascaphus truei* and *A. montanus*[1]) live in cold, rocky streams in the Pacific Northwest and northern Rocky Mountains (Nussbaum et al. 1983) of the USA and in southwestern Canada. Although important to understanding the species' habitat use, population dynamics, gene flow, and recolonization abilities, *Ascaphus* movements are not well documented. Mark-recapture studies directed at detecting movements of transformed *Ascaphus* have concluded that site fidelity is high among mature individuals (Daugherty and Sheldon 1982a) or have been inconclusive (Metter 1964a). Three reports suggested that transformed frogs migrated seasonally; however, direct evidence of movement was lacking (Metter 1964a; Landreth and Ferguson 1967; Brown 1975). Such inconsistencies could reflect either shortcomings in the studies or spatial and temporal variations in movement patterns.

Thermal tolerances and tolerance ranges of *Ascaphus* are lower than for any other anuran studied in North America (reviewed by Claussen 1973). Reports of *Ascaphus* occurrence are generally from streams with maximal temperatures not exceeding 16°C (Franz and Lee 1970; Welsh 1990). Laboratory experiments suggest that thermal tolerances vary among the life history stages. Critical examinations of whether temperature actually limits *Ascaphus* distributions are lacking.

In Rocky Mountain *Ascaphus* populations, individuals transform at age 4, first mature at age 8 and can live for 14 or more years (Daugherty and Sheldon 1982b). The frogs typically mate in the fall (but see Wernz 1969), and females retain sperm until the following July when they lay eggs (Metter 1964b). Eggs usually hatch in late summer, but larvae apparently remain in the nest site until the following summer (Metter 1964a; Brown 1975). This implies that eggs and larvae experience the thermal regime at the nest site throughout an entire year.

Incidental to a study of introduced Brook Trout (*Salvelinus fontinalis*) in two Montana streams (Adams 1999), we made new observations on *Ascaphus* seasonal movements and occurrence in warm water temperatures. We subsequently assessed *Ascaphus* relative abundances and water temperatures throughout one stream-lake network to determine how water temperature was related to summer distributions of each life stage and to timing of downstream frog movements.

[1]Nielson et al. (2001) recommended that inland populations of Tailed Frogs be recognized as a distinct species (*Ascaphus montanus*). Minor inconsistencies between our text and the existence of two distinct *Ascaphus* species occur because our paper was already in press when we read Nielson et al. (2001).

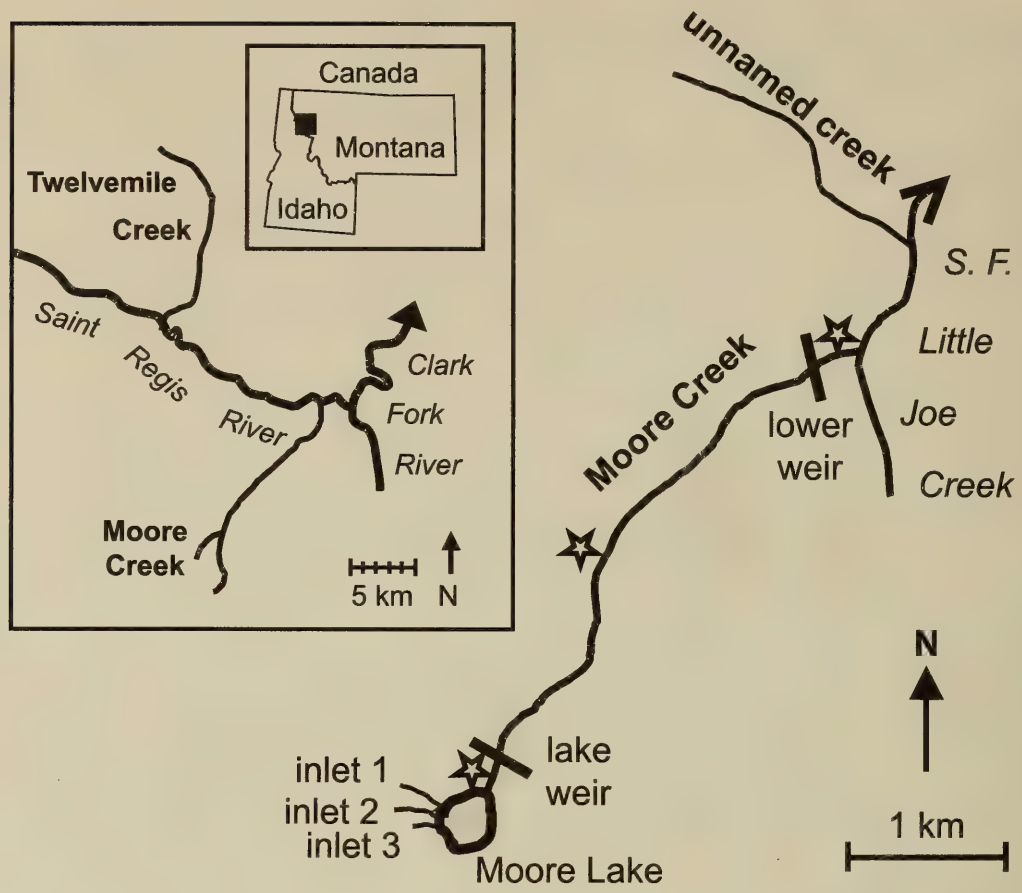

FIGURE 1. Locations of Moore and Twelvemile creeks in Mineral County, Montana, USA, and detail of Moore Creek showing locations of weirs (bars) and temperature recorders (stars). The lake weir was about 75 m downstream of the lake outlet and 5 m downstream of the upper temperature recorder. The lower weir was 120 m upstream of the confluence with South Fork Little Joe Creek.

Materials and Methods

Moore Creek (St. Regis River drainage, Mineral County, Montana, 47°11'N, 115°15'W) is 3.2 km long and is fed by Moore Lake, a 16-m deep, 5.3 hectare, headwater lake at 1620 m elevation. About 320 m of shoreline separates the closest of three, small, lake-inlet streams from the outlet stream (Figure 1). During late summer low flows, average wetted stream widths ranged from 1.8 m near the lake outlet to 3.2 m near the mouth, channel slopes ranged from 10 to 19%, and average maximum pool depth near the lake outlet was 0.23 m. Riparian vegetation was predominantly Western Redcedar (*Thuja plicata*) forest. Twelvemile Creek is larger, longer (22.6 km), and more moderately sloped than Moore Creek with wetted widths ranging from 1.8 to 9.6 m in summer and channel slopes from 1.3 to 8.1 %.

We intermittently counted Tailed Frogs trapped at two weirs in Moore Creek (Figure 1) from 6 August to 9 October 1997 (dates shown in Figure 2) and at four weirs in Twelvemile Creek from July through late September 1997. We checked traps every 2 to 3 days during operation, and the longest period without counting frogs was 12 to 28 September, 1997. The weirs, constructed of 6.35 mm hardware cloth, consisted of two traps facing in opposite directions and connected to each other and to shore by a fence (see Figure 1b in Gowan and Fausch 1996). An apron buried in the substrate prevented animals from easily passing under the weir. Each trap box was a 60 × 60 × 60 cm cube with a funnel extending almost to the back. Large rocks in the traps provided shelter and velocity refugia for captured animals, and lids minimized predation. After identification, animals were released beyond the weir in the direction they were moving when trapped.

We located *Ascaphus* via snorkeling and electrofishing targeting Brook Trout in Moore and Twelvemile creeks in 1997 and via visual surveys targeting *Ascaphus* in Moore Creek in 1998. In July 1998, students assisted with day and night searches for *Ascaphus* along sections of the lake inlet streams, the lakeshore between Moore Creek and the inlet, Moore Creek, and an unnamed creek near Moore Creek (Figure 1). We performed timed searches, turning over streambed rocks and visually scanning both the streambed and stream banks within 2 meters of the stream. The results are intended only for describing *Ascaphus* distribution and for a qualitative comparison of relative densities among reaches.

The lakeshore, one inlet stream, and the uppermost Moore Creek reach were again searched during the night (and Moore Creek also during day) of 7–8 October 1998.

Hobo-Temp® data loggers recorded stream temperatures from 31 July 1997 to 8 October 1998 (with several gaps) at three locations each in Moore (Figure 1) and Twelvemile creeks. Using a digital thermometer, we took a longitudinal temperature profile in Moore Creek downstream of the lake outlet on 28 July 1998 and took focal point temperatures at some *Ascaphus* locations.

Results and Discussion

Adult movements

At the lake weir in Moore Creek, we trapped 32 frogs moving downstream and one moving upstream. As the trapping period progressed, the number of adult *Ascaphus* moving downstream into the trap increased from no frogs for the period of 7 August through 3 September 1997 to nine frogs on 6 October, three days before the weir was removed (Figure 2). The sex ratio of captured frogs was male biased (chi square = 6.1250, p = 0.0133).

The timing of frog captures coincided with a drop in water temperature (Figure 2). The frogs began moving downstream into the trap when average daily stream temperatures dropped below 16°C, and most were captured when average temperatures fell below 14°C (Figure 2). Whenever frogs were recorded in the trap, the maximum daily temperature had not exceeded 16.5°C during at least one day of the two-to-three-day trapping interval.

The pattern of frog captures suggests that a directed, seasonal migration was occurring in upper Moore Creek. The seasonality of the movement is clear from the complete absence of any frogs in the downstream trap for at least the first month of operation. Although there was unquestionable directionality of capture in the traps, concluding that a downstream migration was actually occurring depends on two assumptions: (1) that the weir was not biased against capture or retention of frogs moving upstream, and (2) that the frogs were not moving upstream over land.

We caught no frogs at the lower weir in Moore Creek or at any of the weirs in Twelvemile Creek, although the frogs and larvae were present throughout both creeks (Figure 3) (Franz 1970; S. Adams, personal observation). Thus, *Ascaphus* movement patterns can vary not only among, but also within, streams. The limited literature on *Ascaphus* movements also indicates that movement patterns may vary considerably among drainages. Daugherty and Sheldon (1982a) found no evidence of seasonal or directed movements by mature Tailed Frogs in

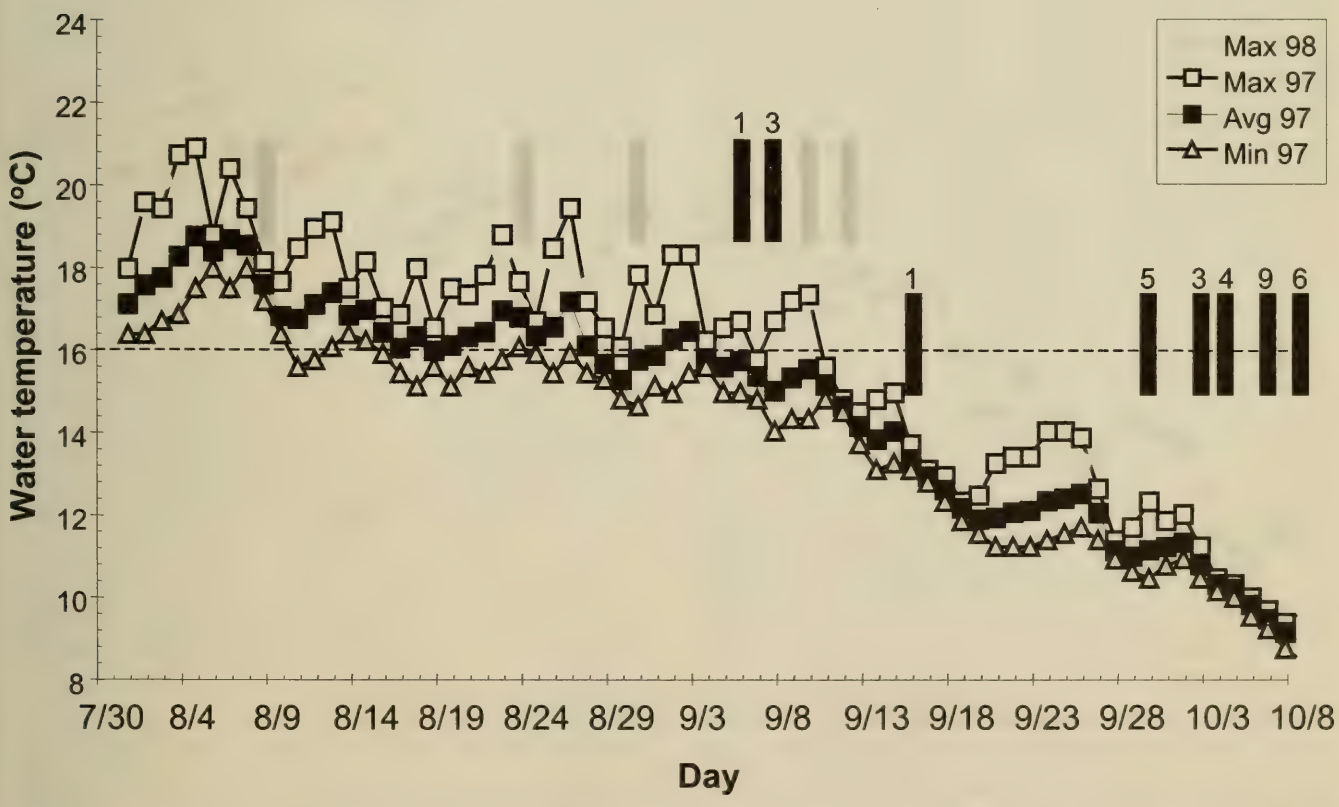

FIGURE 2. Average (avg), maximum (max), and minimum (min) daily stream temperatures 5 m upstream of the "lake weir" in Moore Creek, Montana, 1997 and 1998. Vertical bars indicate dates in 1997 when frogs were counted in traps at the "lake weir". Grey bars represent the absence and black bars the presence of frogs moving downstream. Each bar represents 2 to 3 days of trapping. Numbers of frogs counted are indicated above bars.

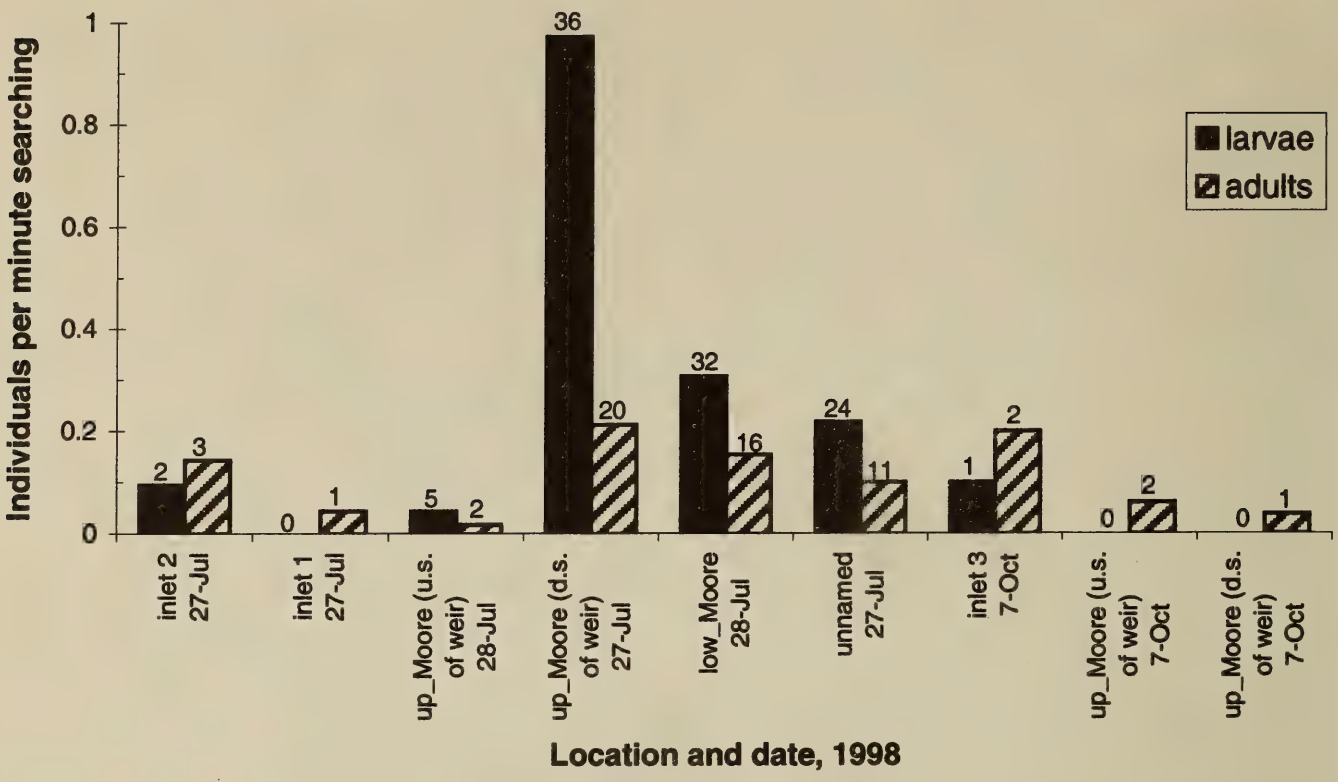

FIGURE 3. Numbers of *Ascaphus* larvae and adults per minute spent searching by each team during night surveys. Numbers above bars are the total numbers of individuals observed during each survey. Inlet 3 was surveyed only in October. u.s. = upstream; d.s. = downstream.

Butler Creek (Montana) and concluded that the frogs exhibited extreme philopatry; however, their annual summer sampling period may have ended too early to detect an autumn migration. By contrast, based on seasonal changes in densities of adult *Ascaphus*, Metter (1964a) hypothesized that adults moved from the Touchet River (Washington) into more shaded tributaries in the late summer. In the Palouse River (Idaho) and tributaries during the same time period, though, he found no seasonal differences in frog densities. Brown (1975) observed aggregations of up to 20 females in "small, shallow tributaries" of Razor Hone Creek, Washington, in late July and suggested that females may move into the warmer tributaries to lay eggs. However, evidence of actual upstream movements was lacking. Landreth and Ferguson (1967) suspected that frogs moved downstream out of small, intermittent creeks to the Lostine River, Oregon, to mate, but again, had no direct evidence of migration. If Tailed Frogs migrate in response to local conditions, diverse movements among sites would be expected.

Stream temperatures and Ascaphus distribution

The average August stream temperature at the upper Moore Creek temperature recording location exceeded 16°C both summers (Table 1). Average daily temperatures exceeded 18°C for at least 5 days in 1997 and 20 days in 1998 (Figure 2), and we likely missed recording many of the warmest days both years. Water temperatures taken during the day and night of 28 July 1998 were 5 to 10°C cooler in the lake inlet streams than in the lake outlet, a pattern that persisted into at least October. Significant water cooling occurred downstream of the lake at both within-reach and whole-stream scales. Water temperatures declined with distance downstream of the lake over 200 m on one warm afternoon (Figure 4), and average August water temperatures at the middle and downstream temperature recording sites were about 7°C cooler than at the site near the lake (Table 1).

Ascaphus larvae and adults were found in all stream sections surveyed except lake inlet 1, where only an adult was found (Figure 3), but none were found along the lake shore. In upper Moore Creek, we observed numerous larvae in water temperatures of 19.5–20.0°C, and several were found in temperatures of 21°C (focal point temperatures). Several

TABLE 1. Stream-scale changes in water temperatures along Moore Creek, Montana, during August 1997 (and 1998 in parentheses). Temperature recording sites were about 0.7, 1.4, and 3.2 km downstream of the lake outlet.

Location	Average	Minimum	Maximum	Maximum daily range
upstream	20.9 (22.8)	16.9 (18.4)	14.6 (15.2)	3.9 (4.1)
middle	12.6	9.7	7.1	2.2
downstream	12.5 (13.9)	10.0 (10.7)	7.5 (7.8)	2.6 (2.5)

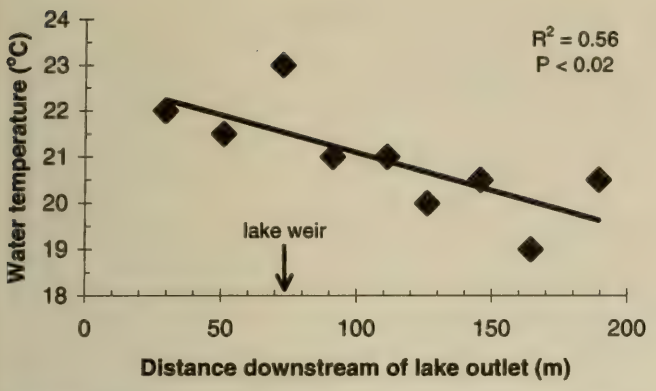

FIGURE 4. Reach-scale changes in water temperatures within 200 m of the Moore Lake outlet. Temperatures were taken on 28 July 1998 between 1235 and 1410 hours, beginning at the outlet and proceeding downstream.

adult frogs also occupied water that was between 19 and 21°C, although most frogs we found were at least partially out of the water.

Maximum stream temperatures in upper Moore Creek were 4.6°C higher than the highest temperature (18.2°C) we found reported where adult *Ascaphus* occurred in nature (Landreth and Ferguson 1967). Reported tolerances of transformed *Ascaphus* in experimental settings are inconsistent but suggest that the frogs may tolerate temperatures of 20°C (Landreth and Ferguson 1967) to 24°C (Claussen 1973). However, low frog densities in the warmest stream reach relative to other reaches and movement through the warmest reach in the fall suggest that high summer temperatures near the lake outlet created an unfavorable summer environment for the frogs.

Ascaphus larvae have been reported in sites with higher water temperatures than have transformed frogs, but not as high as those in upper Moore Creek. Low densities of *Ascaphus* larvae occurred in deforested watersheds of Mount Saint Helens (Washington) where average maximum and mean stream temperatures were 19.5 and 14.4°C, respectively, in late summer (Hawkins et al. 1988). Although maximum summer temperatures in the Washington streams were nearly as high as in upper Moore Creek in 1997, average temperatures were considerably lower. In laboratory experiments larvae survived for a day at 22°C (Metter 1966) and sometimes occupied such temperatures in a thermal gradient (de Vlaming and Bury 1970).

We found a deeply buried nest of *Ascaphus* eggs near the lake weir in Moore Creek on 30 July 1997. On 28 July 1998, we discovered a second nest shallowly buried in a riffle about 30 m downstream of the weir. The majority of embryos appeared viable in both nests. Water temperature in the middle of the pool containing the first nest was 17.4°C at the time of egg collection; however, cold ground water seeping through a bedrock fissure in the substrate less than 1 m upstream of the nest probably moderated temperatures at the nest microsite. When we found the second nest, water temperature was 20.2°C at the nest site and 20.9°C at the opposite side of the pool. *Ascaphus* embryos developed normally in laboratory experiments at temperatures between about 5.0 and 18.5°C, but not at higher temperatures (Brown 1975).

Thermal Complexity

We documented *Ascaphus* response to the spatially complex temperature patterns in upper Moore Creek at both the reach and microhabitat scales. The relative density of both larvae and adults was much higher downstream of the lake weir, where water was cooler, than upstream during July 1998 (Figure 3). However, the relationship between water temperature and *Ascaphus* densities may be confounded by the higher density of Brook Trout upstream than downstream of the weir (unpublished data). The largest aggregation of adult frogs (6 frogs) found was at a cold water pocket (about 9 cm^2) in a mossy bank adjacent to a stream pool. Water temperature was 20–21°C in the pool but was 5.3°C in the pocket. No frogs were found in or along the warmer areas of the pool.

The timing and location of frog captures in weirs suggests that many frogs avoided high water temperatures by migrating. No frogs from upstream of the lake weir were captured until temperatures declined to levels more typically associated with Tailed Frog use. Although two frogs were found in the warm waters upstream of the weir in the summer, higher frog densities occurred in the cold, lake inlet streams (Figure 3). At the other five weirs, stream temperatures remained below 16°C throughout summer 1997, and we found no evidence of migration.

We hypothesize that many of the frogs captured in the lake weir spend the summer in the cold, lake inlet streams (and perhaps in spring seeps around the lake shore), thereby avoiding localized, high summer temperatures in the outlet stream. When lake surface, outlet stream, and air temperatures cool in the fall, the frogs migrate through or around the lake and down the outlet creek to mate and overwinter. Because of their small size, the inlet streams may not provide sufficient overwinter or nesting habitats that are evidently available in the outlet stream. The *Ascaphus* that remain in the warmest reach during summer may persist due to the availability of cool refugia.

Further behavioral studies would be necessary to determine if individuals rely on cool microsites to limit their overall thermal exposure in warm stream reaches; presently, we cannot conclude that occurrence of individuals in warm water implies long-term tolerance of such temperatures. Behavioral responses to thermal heterogeneity and other vari-

able habitat features may help explain the diversity of movement patterns reported in the literature. Future studies of *Ascaphus* movements could benefit by accounting for seasonal changes in habitat suitability and by quantifying in-stream movements rather than focusing primarily on terrestrial movements.

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Prey and Reproduction in a Metapopulation Decline Among Swainson's Hawks, *Buteo swainsoni*

JOSEF K. SCHMUTZ,[1] C. STUART HOUSTON,[2] and SAMUEL J. BARRY[3]

[1]Centre for Studies in Agriculture, Law and the Environment (CSALE), University of Saskatchewan, 51 Campus Drive, Saskatoon, Saskatchewan S7N 5A8 Canada; e-mail: schmutzj@duke.usask.ca
[2]863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada; e-mail: houstons@duke.usask.ca
[3]Canadian Wildlife Service, Environment Canada, 4999-98 Avenue, Edmonton, Alberta T5B 2X3 Canada; e-mail: sam.barry@ec.gc.ca

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Populations and productivity of Swainson's Hawks (*Buteo swainsoni*) have declined for a decade at two study areas (Hanna, Alberta, and Kindersley — Alsask, Saskatchewan) near the northern edge of their Great Plains breeding range. Near Hanna, reproduction in successful nests appeared stable through 1990 and then declined by 31%, followed by a hawk population drop in 1995 and 1996. In Saskatchewan, reproduction began to decline in 1988 and reached unprecedented low levels in 1993 and 1996, followed by a noticeable drop in hawk populations beginning in 1994. In both areas, Richardson's Ground Squirrels (*Spermophilus richardsonii*), the hawks' main prey, have declined drastically in numbers, forcing the hawks to prey more often on ducklings, songbirds and corvids. Forty Swainson's Hawks, marked as nestlings, bred on or near the Hanna study area, including five which moved from Saskatchewan. Recruitment of known-age breeders at Hanna was low at 4.4% of the breeding population, perhaps because the open prairie, which lacks geographic barriers, facilitates wide dispersal. The observed declines of this hawk and other species of grassland birds are of interest because they coincided with pervasive changes in the prairie ecosystem, especially an increasing use of biocides and fertilizers.

Key Words: Swainson's Hawk, *Buteo swainsoni,* Richardson's Ground Squirrel, *Spermophilus richardsonii*, mixed-grass prairie, plant succession, population dynamics, predation, Saskatchewan, Alberta.

Breeding bird surveys in western Canada have shown statistically and biologically significant declines in grassland bird species, including Sprague's Pipit (*Anthus spragueii*), Loggerhead Shrike (*Lanius ludovicianus*), Northern Harrier (*Circus cyaneus*), Killdeer (*Charadrius vociferus*), Burrowing Owl (*Athene cunicularia*), Short-eared Owl (*Asio flammeus*), and Western Meadowlark (*Sturnella neglecta*) (Houston and Schmutz 1999). The Burrowing Owl (Clayton and Schmutz 1999) and Greater Sage-grouse (*Centrocercus urophasianus*) (Connelly and Braun 1997) are in danger of following the Greater Prairie-Chicken (*Tympanuchus cupido*) on the path to extirpation from the Canadian prairies.

Recent unexplained declines in numbers of the Richardson's Ground Squirrel (*Spermophilus richardsonii*), were quickly followed by a decline in productivity and then in numbers of the Swainson's Hawk (*Buteo swainsoni*). We undertook an analysis of two large data sets of this quintessential grasslands hawk and its main prey species, and examined the amount of grassland habitat, numbers of trees, and hawk dispersal. Data were accumulated in two different agricultural landscapes (ranching and cereal crop production) over 18 and 25 years, respectively. Breeding Swainson's Hawks, but not Ferruginous Hawks (*Buteo regalis*), have adjusted well to as much as a 90% conversion of grasslands to cropland (Schmutz 1989).

Once maintained by fire and by Bison (*Bison bison*) and Pronghorn (*Antilocapra americana*) grazing and browsing, and more recently by domestic grazers in an emerging ranching economy (Jameson 1986), much of the grassland in our study region has been lost to dry land crop production (Rowe 1987). The Canadian prairies have been called "one of the most altered habitats in the world," so much so that the sustainability of agricultural practices themselves has been questioned (Anderson et al. 1991).

Study Areas

Both study areas are in the dry mixed grass ecoregion of the northern Great Plains (Figure 1; Strong and Leggat 1992). Native plant species in the gently undulating landscape are adapted to severe moisture deficits in mid- to late summer. Trees and shrubs used by the hawks for nesting include Trembling Aspen, *Populus tremuloides*, Chokecherry, *Prunus virginiana*, Saskatoon, *Amelanchier alnifolia*, Buffaloberry, *Shepherdia argentea,* Prickly Rose, *Rosa acicularis,* and willows, *Salix* spp., growing naturally since the control of prairie fires (Houston and Bechard 1983). The hawks also use introduced trees planted for shade and windbreaks (Manitoba Maple, *Acer negundo,* Green Ash, *Fraxinus pennsylvanica*, American Elm, *Ulmus americana,* Caragana, *Caragana arborescens*, and hybrid poplar, *Populus* sp.).

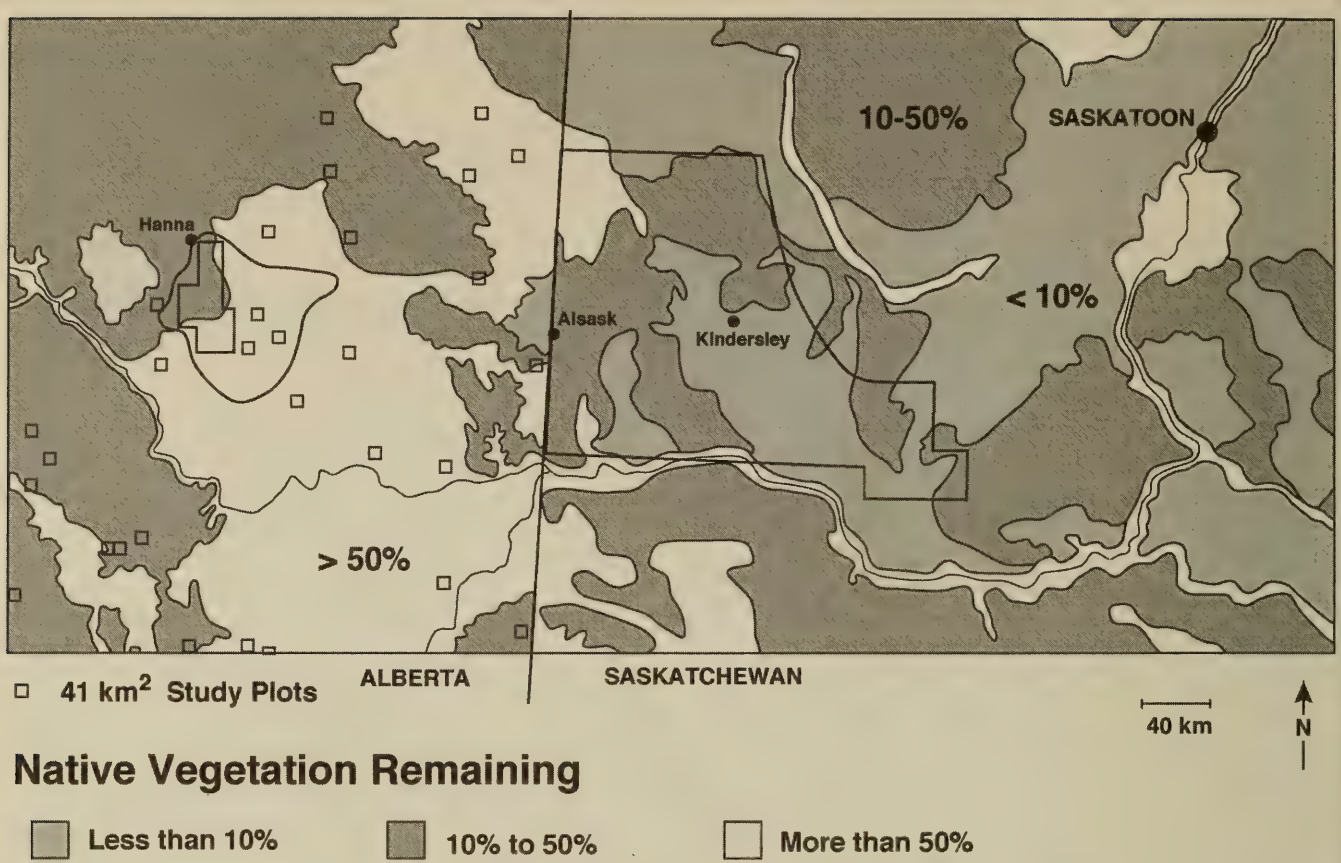

FIGURE 1. Percent of native vegetation in the two study areas. Boundaries of the completely searched Hanna study area are within a larger study perimeter. Of the 78-83 randomly selected study plots used, 30 lay within the region shown. The Saskatchewan area was searched opportunistically.

Alberta: The town of Hanna (51° 38′N, 112° 33′W) is near the northwest corner of the study area, which encompassed 480 km^2 in all years except 1975 (southern 335-km^2 portion) and 1983 (southern 326-km^2 portion). This ranching area, with approximately 85% mixed grass remaining, was monitored intensively from 1975 through 1978 and from 1983 through 1996. During summers (May–August) in the mixed grass ecoregion of Alberta, the mean temperature overall was 16.2°C (range 8.7–23.6°C). Average summer rainfall was 15.6 cm (8.8–23.3 = 25% & 75% percentiles; Strong and Leggat 1992). Here, at the southern edge of the southward-advancing aspen parkland, expansion of trees has been noticeable since the mid-1970s. Some Swainson's Hawks nested in *P. tremuloides* that grew during this study in previously treeless sites.

Saskatchewan: Kindersley (51° 28′N, 109° 09′W) is the largest town in the study area, and Alsask (51° 21′N, 109° 59′ W), is at its western margin (Figure 1). This area was sampled mainly from 1972 through 1996. Near Kindersley, the land has been extensively altered for cereal crop production (< 10% native habitat), whereas Alsask was intermediate (10–50% native). On the large pastures near Kindersley, trees remaining in deserted farmstead shelterbelts continue to die out. Mean July temperatures were 18.8°C and annual rainfall was 25.1 cm (Padbury and Acton 1994).

Methods

In Alberta, a complete search for nests was carried out each year on the Hanna study area, and thrice on randomly selected study plots throughout southeastern Alberta (Table 1). Near Kindersley, Saskatchewan, Swainson's Hawk nest finding was a by-product of Ferruginous Hawk banding in late June.

Southeastern Alberta hawk population estimate

In 1982, a count of nesting buteos for population monitoring was done on 80 randomly selected 41-km^2 study plots, a portion of which are depicted in Figure 1. The same protocol was followed in 1987, but in 1992 five new plots were added. The total number of plots searched was 80 in 1982 (Schmutz 1984), 78 in 1987 (Schmutz 1989), and 83 in 1992.

Alberta (Hanna) Study

Except in 1978 and 1983, JKS was present on the study area from late May or early June through early August. Each year, during 10 to 15 days in June, JKS searched by motorcycle all clumps of trees and shrubs, artificial nests, and eroded slopes. A 45-km^2 northern portion of the study area was searched in early July.

TABLE 1. Types of studies carried out on Swainson's Hawks and Richardson's Ground Squirrels on the study areas in Alberta and Saskatchewan, and their periods.

	1967-19 74	19 75	19 76	19 77	19 78	19 79	19 80	19 81	19 82	19 83	19 84	19 85	19 86	19 87	19 88	19 89	19 90	19 91	19 92	19 93	19 94	19 95	19 96
Alberta (Hanna)																							
Ground squirrel:																							
dispersal/density		X	X																				
strychnine sales	X	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X				
burrow counts		X	X																				X
Total nest count		X	X	X						X	X	X	X	X	X	X	X	X	X	X	X	X	X
Banding: CWS bands	X[1]	X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
colour (>25/yr)											X	X	X	X	X	X	X						
Dispersal/survival											X	X	X	X	X	X	X	X	X	X	X	X	X
Competition		X	X	X																			
Strychnine impact															X								
Alberta Pop. estimate									X					X					X				
Saskatchewan																							
Banding: CWS bands	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
colour															X	X	X	X	X	X	X	X	

[1]By Richard W. Fyfe and colleagues

From 1975 through 1977, we recorded nest contents in late May by climbing to the nest or using a mirror on a pole. Starting in 1983, all nests of Swainson's Hawks on the study area were approached during the June search, but only until the occupant could be identified to species. In most cases nests were not closely inspected until the nestling period (July) to minimize chances of nest desertion (Houston 1974). For this reason, clutch size was often not known.

To aid interpretation of a failed reproductive attempt, nests were carefully inspected. For a reproductive attempt to be counted, the nest base had to be complete, the cup lined, and the lining flattened as by a hawk's body during laying or incubation. Often nests had been added to and sometimes even completed but not flattened. The presence of down feathers in the nest material was not a reliable indicator of laying or incubation. Nests in which young had died during the second half of the nestling period generally showed a trampled nest rim, droppings, and a nest cup filled with prey remains, pellets, and sprigs of herbaceous plants. Nests in which young hatched but died soon thereafter showed the original deep cup. Often tiny egg fragments from pipping eggs remained lightly buried in the base of the nest cup. Eggs abandoned before hatching were opened and the approximate stage of the arrested development recorded.

For brood counts and banding, nests were visited late in the nestling period in both study areas. We did not adjust the data based on nestling age and survival probabilities (e.g., Mayfield 1975). Instead, a few nests were excluded when brood size was manipulated (e.g., Schmutz et al. 1980), or when nestlings in unusually late nests were less than half-grown (< 2% of nests).

Near Hanna, searching the study area for nests and banding young was a priority in all but two years (Table 1). Aluminum bands were placed on 366 adults and 1968 young, and alpha-numeric colour bands were applied to 236 adults and 1240 young.

Additional avenues of investigation varied (Table 1). We studied competition among buteo species in three summers, 1975 through 1977 (Schmutz et al. 1980), in an area studied by Richard W. Fyfe and coworkers between 1967 and 1974 (Schmutz et al. 1991). After a four-year hiatus, we resumed work on the Hanna study area from 1983 through 1996.

In 1984, 1985, and 1986, we live-captured 196 adults (Bloom et al. 1992) for a survival and site-fidelity study; another 170 adults were captured during other years between 1975 and 1996. Reading colour bands, achieved on 510 occasions, was thereafter a priority.

The number of prey records, after young had hatched, varied between years, depending on the nature of other studies underway. In recent years, the

small prey sample in both study areas was primarily influenced by the decline in the number of nests, and presumably because the hawks were so food-stressed that their food was consumed quickly. In addition to species, sex and age, the portion of prey still available for consumption was recorded in the field and converted to weight using prey weights — either taken from the literature or locally recorded. Ground squirrel weight varied by age and sex throughout the season (Schmutz 1977). For whole prey the consumable portion was assumed to be 85%, and proportionately less for incomplete remains.

At Hanna, we have three indices of ground squirrel abundance, in addition to the number of ground squirrels found in nests. One was a mark-recapture ground squirrel study done to document dispersal and mortality in 1975 and 1976. The second was burrow counts. The third was a 25-year record of strychnine sold by the "Special Areas Board" (Gorman 1988). Strychnine was sold at a consistent low cost as a service to the farming and ranching community, hence cost did not affect the volume used. The poison data were independent of the questions addressed here, representative of a large municipality encompassing 76 686 km^2 and involving over 100 ranchers.

Strychnine was purchased in liquid form, Gopher Cop®, and used to coat oat bait. A person then dropped a spoonful of bait down each burrow entrance while walking or driving an all-terrain vehicle around field edges including the grassy borders, around garden plots, in corrals and through "calving pastures." More poison was purchased in years of high ground squirrel density.

In view of ground squirrel ecology and local poisoning practices, demand for poison varied for two reasons. When survival during hibernation was high, the density of breeding females was high; males suffered a disproportionately high mortality and represented only 19% of the adult population (Schmutz et al. 1979). Also, demand for poison could be high when the number of young produced was high. Beginning in early to mid-June, young disperse and dig new burrows or re-use formerly vacant burrows coinciding with crop in early stages of growth. We view the poison data as an index that is sensitive to large and widespread changes in the number of ground squirrels (Schmutz and Hungle 1989).

Saskatchewan Study

CSH banded Swainson's Hawks intermittently from 1944 through 1972. From 1973 on, he concentrated most of his banding on and near large pastures near Kindersley, visiting twice each summer to apply leg bands and to monitor productivity. Most incubating Swainson's Hawk pairs were located during Ferruginous Hawk banding in June; all such nests were revisited for banding in mid- to late July. Additional Swainson's Hawk nests were found en passant along intervening roads and trails, and by visiting occupied sites from preceding years. Prey remains were recorded during a single banding visit in late July. This study area was not completely searched and had no well-defined boundaries. The focus was on number of nests visited, not density per unit area. From 1988 through 1995, 684 double-rivet anodized alpha-numeric bands, manufactured by A-Craft Sign and Nameplate Co., 10342 59 Avenue, Edmonton, Alberta T6H 1E6, were applied on each nestling's leg opposite that carrying the usual aluminum band.

CSH also studied, but less intensively and less regularly, Swainson's Hawk nesting in parkland areas near Saskatoon.

Results

Southeastern Alberta hawk population survey

Hawk distribution on the randomly selected 41-km^2 study plots was influenced by cultivation and tree availability (Schmutz 1989). Of 780 Swainson's Hawk nests recorded on or off plots in the three survey years, site descriptions were transcribed from field notes for 377 nests. For these, planted shelterbelts supported nearly as many nests (139) as single trees or clumps of aspens (145) and more than native shrubs (79; Table 2).

TABLE 2. Nest substrates (n = 378) used by Swainson's Hawks in the mixed, moist mixed and fescue grassland ecoregions in southeastern Alberta, in 1982, 1987 and 1992. Nests found in the perimeter of randomly selected study plots are included.

	"Natural"				Cultural		
Grassland	Aspen	Cotton-wood	Shrubs[1]	Ground	Shelter-belt	Artificial nest	Building/ windmill
Mixed	82	2	31	1	53	2	1
Moist mixed	39	6	30	0	37	2	0
Fescue	24	0	18	0	49	0	1
Total	145	8	79	1	139	4	2

[1]Willow (*Salix* spp.), Chokecherry (*Prunus virginia*), Saskatoon *(Amelanchier alnifolia)*, Buffaloberry *(Shepherdia argential)*, and Prickly Rose *(Rosa asicularis)*.

TABLE 3. Data from the Swainson's Hawk population studied near Hanna, Alberta, 1975–1996. When the size of the study area was reduced, the northern portion was not searched.

		Nests					Nests Abandoned			Clutch		Nests	Brood			Off
	Area (km^2)	Incom-plete	Com-pleted	/100 km^2	Outcome known	Nest fell	before hatch	after hatch	stage unkn.	#	Nests	with young	#	Nests	SD	area nests
1975	335	3	38	11.34	34	2	3	2	0	2.50	24	27	2.13	23	0.63	1
1976	480	4	77	16.04	72	3	8	3	2	2.45	29	56	1.94	48	0.84	9
1977	480	5	70	14.58	49	3	4	1	3	2.00	16	38	2.00	37	0.78	19
1978	~100												1.87	15	0.74	
1983	326	2	43	13.19	37	0	0	2	4	2.00	3	31	2.17	30	0.87	2
1984	480	7	71	14.79	70	3	4	7	8	1.88	8	48	1.88	48	0.76	55
1985	480	8	84	17.50	81	2	5	7	11	2.60	5	56	2.16	56	0.68	94
1986	480	11	104	21.67	102	11	6	8	5	2.46	13	72	2.17	70	0.85	75
1987	480	8	97	20.21	94	4	8	5	1	2.68	31	76	2.26	76	0.80	22
1988	480	4	103	21.46	98	8	7	4	10	2.73	37	69	1.96	69	0.86	50
1989	480	21	64	13.33	63	2	3	4	4	2.25	4	50	1.92	50	0.67	11
1990	480	9	84	17.50	81	8	7	11	4	1.75	4	51	2.06	51	0.84	13
1991	480	16	60	12.50	58	1	5	10	3	1.33	3	39	1.33	39	0.62	8
1992	480	8	69	14.38	65	3	8	5	3	1.75	4	46	1.50	46	0.69	4
1993	480	15	73	15.21	72	7	8	23	6	2.31	13	28	1.11	28	0.31	8
1994	480	8	63	13.13	63	4	2	11	10	2.60	5	36	1.69	36	0.79	7
1995	480	18	33	6.88	33	0	2	14	6	2.00	2	11	1.25	8	0.44	16
1996	480	16	32	6.67	32	2	6	4	5	2.00	8	15	1.40	15	0.51	7
1975-1985		29	383	14.84	343	13	24	22	28	2.32	85	256	2.03	257	0.73	180
1986-1988		23	304	21.11	294	23	21	17	16	2.67	81	217	2.13	215	0.84	147
1989-1994		77	413	14.34	402	25	33	64	30	2.12	33	250	1.66	250	0.75	51
1995-1996		34	65	6.78	65	2	8	18	11	2.00	10	26	1.35	23	0.48	23
1975-1996		163	1165	14.82	1104	63	86	121	85	2.41	209	749	1.91	745	0.80	401

Nest Densities

Alberta (Hanna): Over 18 years of study by JKS spanning 22 years, nesting areas totalled 1730. Of these, 1165 nests were completed within the study area, and 163 nests were not completed (Table 3). Another 401 nests (1–94 per year) were monitored adjacent to the formal study area.

As was found in the regional survey (Schmutz 1989), Swainson's Hawks near Hanna also favoured cultivated areas. In the peak year, 1986, densities on the grassland block were 14.4 nests/100 km^2, compared to 25.3 nests/100 km^2 in the surrounding mix of rangeland and cultivation. In the lowest density year, this trend persisted with 5.0 nests/100 km^2 in grassland and 7.5 nests/100 km^2 in mixed habitat.

There were four distinct periods in the hawks' population dynamics; two periods of "moderate" numbers (1975-1985 and 1989–1994), interrupted by a period of "high" numbers (1986–1988), followed by a period of "low" numbers (1995–1996) (Figure 2).

Litres of strychnine used varied in parallel with hawk densities during the peak prey years and before (Figure 2, Spearman rho = 0.631, P = 0.029). Overall, however, and without strychnine data for 1993–1996, hawk density and strychnine were not significantly correlated (Spearman rho = 0.445, P = 0.107).

The strychnine data suggested that ground squirrels existed on the Hanna study area in moderate numbers before 1986, peaked in 1986–1988, fluctuated until 1990, and then declined. The ground squirrel low continued beyond 1992, when the poison sales program ended.

Saskatchewan: CSH recorded 1561 nests with young from 1973 on. As a result of increased searching effort, the number of nests increased up to 1987 (Figure 3). Although searching effort remained high and relatively constant in later years, the number of nests found declined in the 1990s. In the most consistently and intensively studied township, north of Kindersley, Jean Harris found 15.4 pairs/100 km^2 in 1990 and 1991; this dropped to 6.4/100 km^2 in both 1994 and 1996.

To approximate the timing of a shift from an increase in number of successful nests to a decrease, we calculated a Spearman rank correlation coefficient for the increasing portion of the plot (Figure 3), separately from the decreasing portion, allowing a three-year overlap. We shifted these periods until the highest combined absolute value of rho was obtained. We thus obtained a Spearman rho of 0.875, $P < 0.001$, for 1968–1988, and -0.692, P = 0.029, for 1986–1996. This suggests that the nest decline began in 1988.

Dispersal, non-breeding floaters and recruitment

Alberta (Hanna): We distinguished between sightings at nests and sightings > 300 m from nests. Of 1483 Swainson's Hawks that were not individually marked and were more than 300 m from the nearest

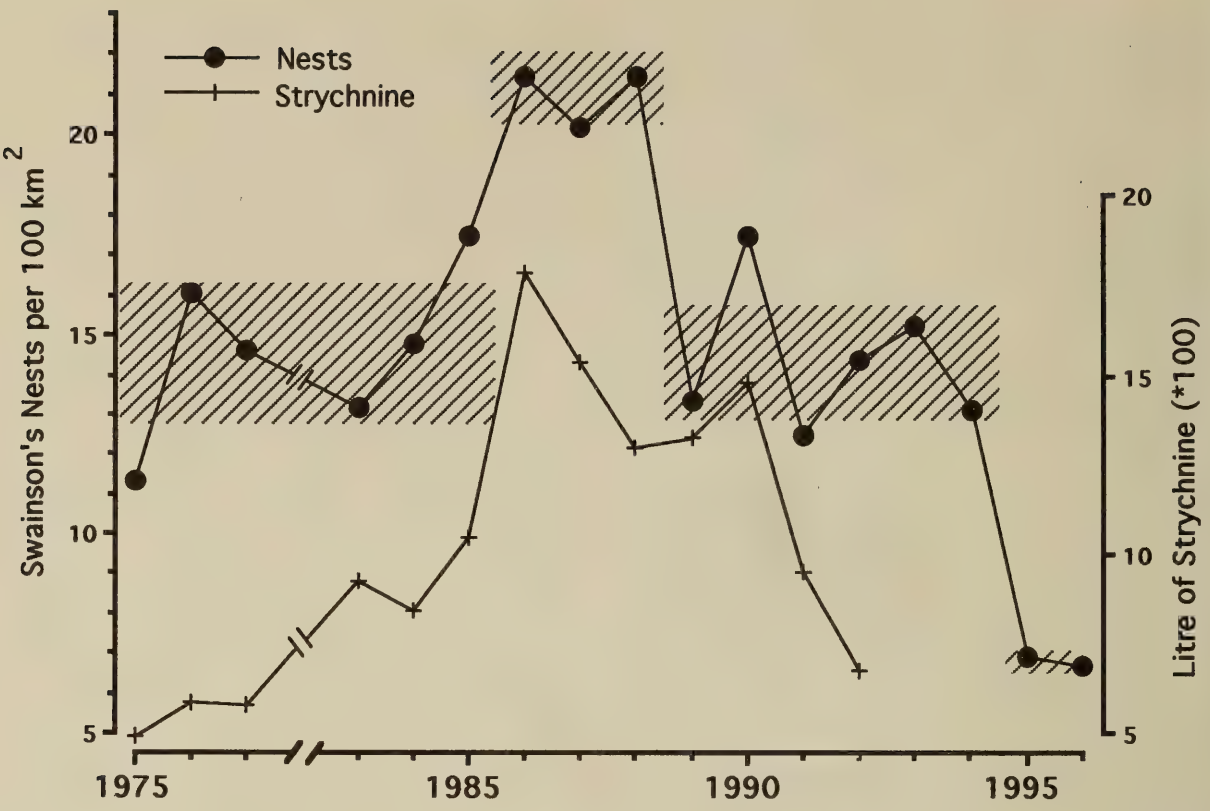

FIGURE 2. Number of nesting pairs of Swainson's Hawks for the Hanna, Alberta study area. Cross-hatched regions span two medium, one high and one low density period, and show 95% confidence intervals. Litres of strychnine poison used to poison ground squirrels are also plotted.

nest, 140 were in close proximity to another and presumed paired (70 pairs). One such pair is noteworthy because it shows that at least some satellite non-breeders pre-select nest sites for use in subsequent seasons. The female was radio-marked on 24 August 1995 (Schmutz et al. 1996). The female and the same male, judging from his plumage, returned to reuse this nest and lay eggs the following year.

An additional 39 hawks existed in six flocks of 4, 4, 5, 5, 10 and 11 individuals, with a mix of adults and subadults. These "satellite" hawks were also presumed to be non-breeding, as few of the marked breeders were ever seen roosting as pairs more than 300 m from their nests (JKS, unpublished data) and communal hunting is not known in this species. All six flocks and 51 (73%) of the 70 non-breeding pairs were recorded during the high ground squirrel years of 1986–1988 (JKS, unpublished data).

In July and August 1995, a seventh flock of 33 Swainson's Hawks was noteworthy. These birds, in adult and sub-adult plumage (Clark and Wheeler 1987), were repeatedly seen feeding in cultivated but fallow fields. Their walking, stalking, and pecking behaviour indicated that they were feeding on insects. As noted in a local newspaper, local residents had repeatedly seen large flocks of hawks that year. Thus, even in a year when conditions for reproduction were poor, the area was sufficiently attractive to hold non-breeders.

Many of the non-breeders appeared to be transients. On the study area, we observed a total of six locally reared and individually marked hawks, including five 1-yr-olds and one 5-yr-old, none of them known to be nesting. Each was sighted only once, even though we made a special effort to relocate them on subsequent days.

Breeding hawks included both locally raised hawks and immigrants. Of 39 adult Swainson's Hawks of known origin that attended nests at Hanna during 1977–1996, 35 had been locally marked as nestlings and four had immigrated 135 to 310 km from near Kindersley, Saskatchewan. The greatest number of recruits (n = 8) was sighted in 1986, when these comprised 4.4% of 182 adults of known banding status at nests on or off the Hanna study area. One five-yr-old local recruit attended an unfinished nest in 1989, and one nine-yr-old was seen in copulation but not recorded thereafter in 1996. The average age of 33 breeders when first encountered was 4.5 yr (range 2–9 yr), from 0 to 45 km from their natal site.

Saskatchewan: From 684 nestling Swainson's Hawks colour-marked in Saskatchewan, there were four sightings by a waterfowl biologist within a month after banding, all within 1 km of the nest. Although in each subsequent year up to 102 adults were seen adequately to detect a colour band on a tibio-tarsus, there were no later local sightings of

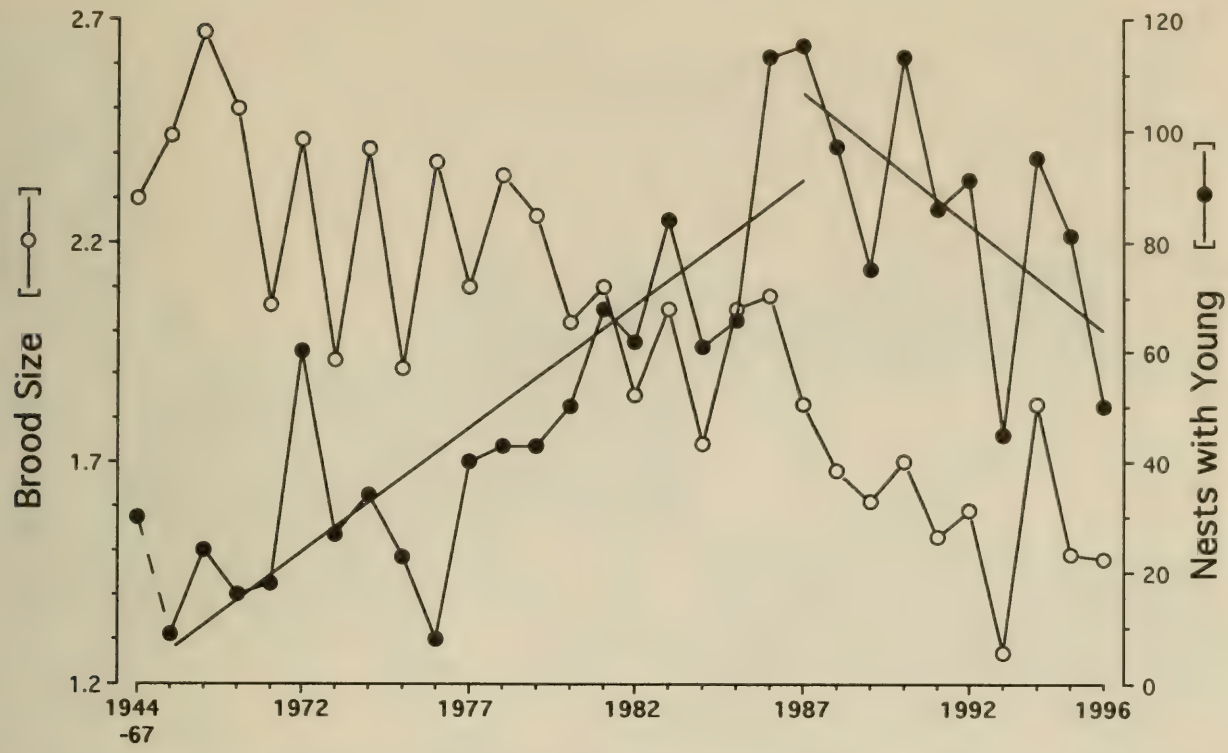

FIGURE 3. Yearly mean brood size and number of nests containing young Swainson's hawks in mid and late July, in Saskatchewan.

colour bands. However, one, 4-T, was read twice by telescope by JKS on the Hanna study area in Alberta, 135 km to the west, at three and seven years after fledging, and another colour-banded hawk was captured and released by a research biologist on 4 June, when almost nine years old, at Caronport, Saskatchewan, 295 km ESE of where banded.

Prey Items in Nests

Swainson's Hawks relied extensively on ground squirrel prey, 60% of items in Alberta and 38% in Saskatchewan (Appendix 1). Beyond ground squirrels, these hawks exhibited a generalist strategy, using prey of at least 52 species in four taxonomic classes. Studies of prey items alone, without pellet analysis in the later years, and without time lapse photography, tend to underestimate small prey (e.g., Simmons et al. 1991). However, nest prey data can be useful to compare trends over time.

The proportion of ground squirrels among prey declined in step-like fashion in both areas, beginning in 1983 in Saskatchewan, and in 1991 near Hanna.

Alberta (Hanna): Before 1991, ground squirrels constituted more prey items than all other prey species together (Figure 4). Later, the proportion of ground squirrel prey declined ($G = 61.95$, $df = 14$, $P < 0.001$). As ground squirrels declined, the smaller size of most substitute prey species resulted in a considerable reduction in prey biomass. Relative prey sizes are 73 to 443 g for all ground squirrel age and sex classes (Schmutz 1977), compared to mice and voles (17 to 26 g) and songbirds and corvids (20 to 450 g) or primarily juvenile waterfowl prey (39 g for juveniles, 565 g for adults taken infrequently). The correlation between ground squirrels present on visits to nests and the estimated grams of prey biomass still available for consumption was high because of the large size of ground squirrels relative to other prey (Spearman rho = 0.738, $P = 0.003$). When converted to biomass, 82% of nest prey and 69% of prey and pellets were ground squirrels, confirming the bulk importance of this prey (Schmutz et al. 1980).

Saskatchewan: Through 1982, prey items were present in 35% of nests when visited; 50% of the prey items were Richardson's Ground Squirrels and 1% Thirteen-lined Ground Squirrels. The proportion of ground squirrels found was significantly lower after 1982 ($G = 28.6$, $P = < 0.0001$, Figure 5). From 1983 through 1996, prey items were found in only 22% of nests, and only 30% of the prey were ground squirrels. With the obligatory switch in diet, ducklings, Horned Larks (*Eremophila alpestris),* and Western Meadowlarks (*Sturnella neglecta*), became important prey items. Some pairs, faced with insufficient food to raise more than one nestling, were feeding the youngest to the oldest ("cannibalism" or siblicide) at the time of the banding visit (Appendix 1). Additional prey included 181 other mammals of 11 species, 211 birds of 38 species, 3 amphibians and 2 reptiles.

Hawk reproductive success

Alberta (Hanna): There was a remarkably close agreement between amount of prey in nests (Figure 4) and brood size in Alberta (Figure 6), presumably representing cause-and-effect.

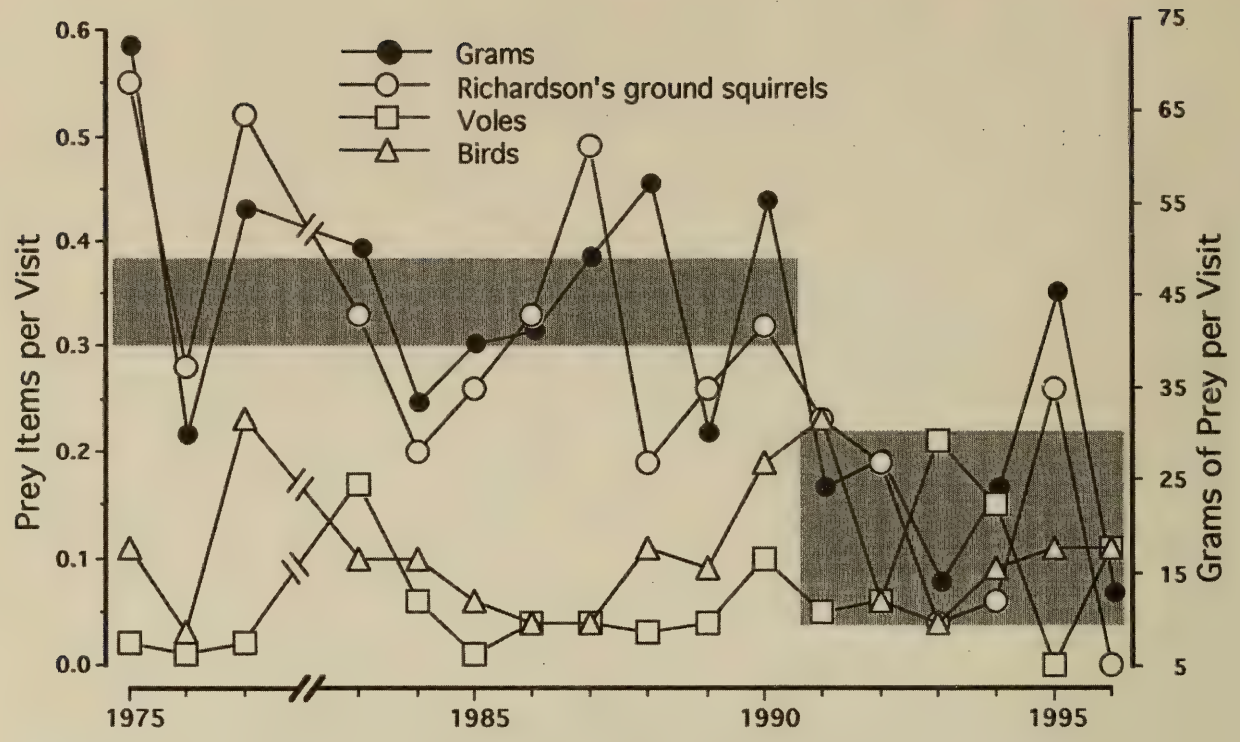

FIGURE 4. Prey items in nests of Swainson's Hawks on the Hanna study area. Shaded regions span the "moderate" and low ground squirrel years (see text), and represent 95% confidence intervals around the respective means.

Brood size departed little from a 2.06-young average during the first 12 years, 1975–1978 and 1983–1990 (Figure 6). During the following six years, average brood size declined by 31% to only 1.42. The number of nests with 1 (n = 158), 2 (n = 215) and 3–4 young (n = 172) was significantly different during 1975–1990, compared to 1991–1996 (101, 32, 10, respectively; G = 88.94, d.f. = 2, $P < 0.001$).

The proportion of nests with young raised to near fledging was 78% from 1975–1990, and 58% from 1991–1996 (G = 42.3, P < 0.001). Nests that fell from trees (Table 3) were excluded from this analysis; this failure category was considered an event unrelated to food. The gap between brood size and a sampling of clutch size widened over time (Figure 6), suggesting that the decline in reproduction was due to a combination of smaller clutches and reduced embryo/nestling survival. The clutch/brood gap in the periods of medium, high, medium, and low densities (see Figure 2), was 0.29, 0.54, 0.46 and 0.65, respectively.

Clutch size, too, was reduced in the low prey years 1991–1996, but brood size was reduced even more severely in those years (Figure 6). Expressing a total 209 clutches as either above or below the grand mean of 2.40, we found that 89 clutches were above and 85 below for 1975–1990, and 10 above and 26 below for 1991–1996 (G = 6.77, P = 0.009).

Saskatchewan: Brood size was > 1.8 (except 1984) through 1987. During four years, 1972, 1976, 1978, and 1979, nests with three young were more common than those with two young. The percentage of nests with three young was 28% through 1987 and then dropped to 11% from 1988 through 1996, while the percentage with one young increased from 29% to 52% in the same periods (Houston and Schmutz 1995b). Brood sizes declined fairly steadily (by 29%) from 2.25 young per successful nest in the 1970s to 1.60 young in the 1990s (Table 4; Spearman rho = -0.868, $P < 0.001$; Figure 3). The least successful year was 1993, when the minimum nest failure rate between mid-June and late July was an all-time high of 61%, and the brood size was an all-time low of 1.27 (1.00 for the only eight successful nests near Alsask). Of 45 successful nests in 1993, adult hawks failed to appear during the banding visit at seven; in response to a decline in ground squirrels, the hawks may have been forced to feed farther from the nest and so did not notice the bander's visit.

We separated subsets for Kindersley and Alsask to show the differences in the timing of declines in brood size. Near Kindersley there was an unexplained increase in brood size from 1976 to 1979 (Figure 7). In 1987, brood size began to decline near Kindersley, and in 1993 near Alsask (Figure 7). [In comparison, at Hanna, Alberta, this decline was first noticed in 1991 (Figure 6)].

The parkland (aspen bluff) areas of Saskatchewan, where Richardson's Ground Squirrel numbers were

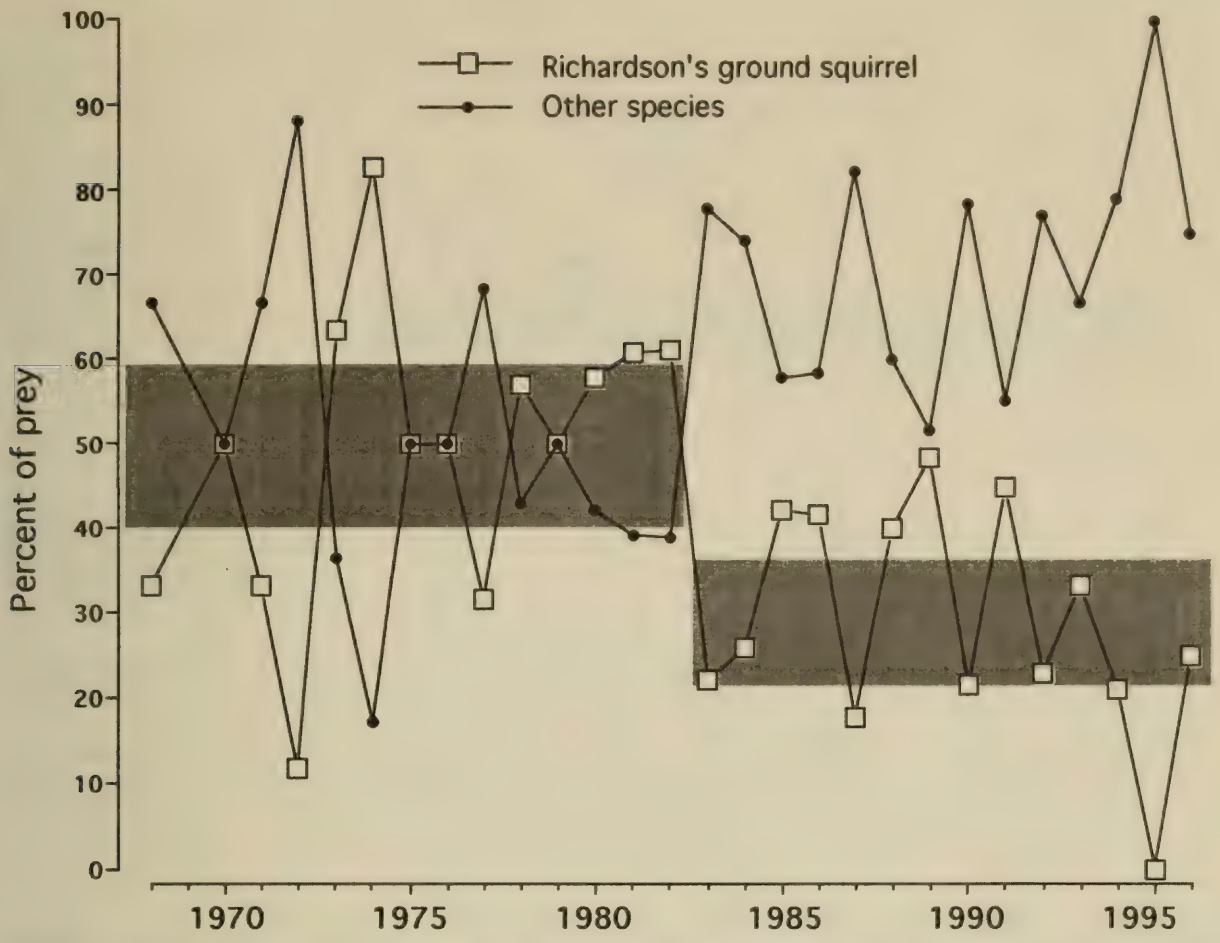

FIGURE 5. The proportion of Richardson's Ground Squirrels in relation to other vertebrate prey in Saskatchewan. The shaded region represents means (50% and 32%) and standard deviation (17 and 11) for two periods of moderate and low ground squirrel use, respectively.

maintained, produced strikingly different results from the more open grassland areas mentioned above. Near Saskatoon, from 1964 through 1987, Swainson's Hawk brood size averaged 2.3 young per successful nest (154 young banded in 67 nests). Brood size dropped slightly to 1.8 (96 young in 52 nests) from 1988 to 1992, then returned to 2.2 (29 young in 13 nests) from 1993 to 1996.

Ground Squirrel abundance

Alberta (Hanna): A direct measure of ground squirrel abundance using mark-recapture was available only for two years. On six 4-ha plots and surrounding areas, 1497 ground squirrels were individually marked. Densities on these selected well-drained study plots ranged from 3.3 to 7.0 squirrels per ha in 1975, and 3.8 to 7.5 in 1976 (Schmutz et al. 1979).

The shift in the 1990s away from ground squirrel prey (Figure 4) was independently supported by a second index of ground squirrel abundance, i.e., counts of used burrows on study plots (Schmutz et al. 1979). In June and July 1975, 23 1-km transects, on which used burrows were counted within 1 meter of a slowly driven motorcycle, yielded on average 11.5 burrows/km. On 25 July 1996, a repeat single 1-km transect on each of the six plots yielded no used burrows, and no ground squirrels; although diminished and locally variable in numbers, ground squirrels were still present sparingly elsewhere on the study area during the 1990s.

Jones (1993) also documented the extreme paucity of Richardson's Ground Squirrels near Brooks and south of Edmonton, Alberta, in 1993. In stark contrast to previous years, he observed extremely few live ground squirrels and no road-kills that year, and found none in nests of Swainson's Hawks that year.

Saskatchewan: Prior to 1988, young Richardson's Ground Squirrels were abundant, with up to 10 encountered per km of prairie trail; road kills were encountered regularly. In contrast, on six days in June and four days in July 1993, CSH drove > 300 km per day in prime Swainson's Hawk habitat, with sightings of only 0–3 ground squirrels per day, and not one road kill. On each of those days, more Red Foxes and Coyotes were seen than ground squirrels, a 100-fold reversal of the previous ratio of ground squirrels to either of these species. Richardson's Ground Squirrels increased slightly over the next two years, though still remaining ≤ 10% of former numbers. In

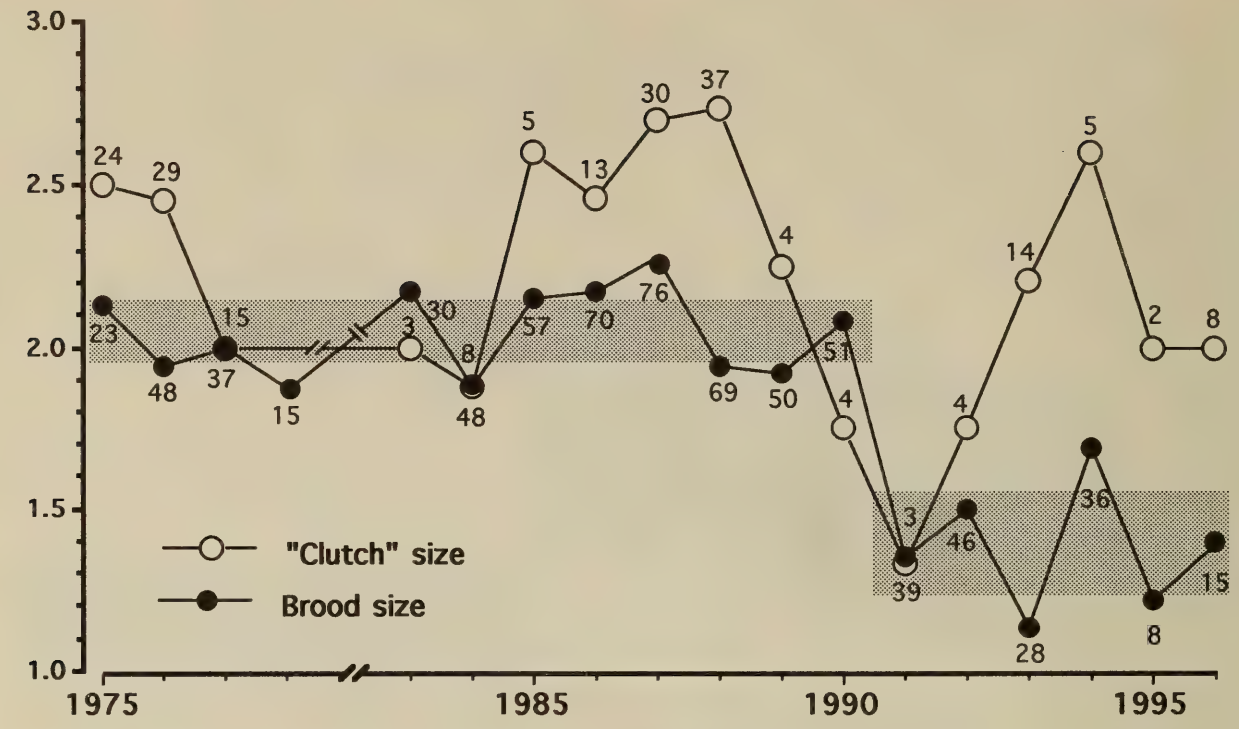

FIGURE 6. Number of young at banding (Brood) and eggs in late hatching nests ("Clutch") of Swainson's Hawks for the Hanna study area. Numerals represent number of nests involved. Shaded regions represent the 95% confidence interval around the respective means. The mean brood size and standard error for periods prior to 1990, after 1990 and for all years were 2.05 ± 0.13, 1.38 ± 0.21 and 1.8 ± 0.36, respectively.

1995, travels of > 300 km each day by CSH recorded, sequentially, 3, 9, 1, 29, 11, and 10 ground squirrels in June, and 2, 10, 3, 1, 1, 14, 2, 0 and 0 ground squirrels in July. From 1992 through 1996, few Richardson's Ground Squirrels were encountered as prey in hawk nests, none at all in 1995.

Discussion

Dispersal

Our study areas included grassland and cropland interspersed with permanent or semi-permanent wetlands in mixed prairie. Both the Hanna, Alberta, and Saskatchewan study areas lie about 200 km south of the northern edge of a large region of western North America occupied by Swainson's Hawks. Some colour-marked breeders at Hanna were recruited locally, but others moved onto the Hanna area from localities outside it, including five from the Kindersley area of Saskatchewan (Houston and Schmutz 1995a). Natal dispersal of Swainson's Hawks across the Canadian prairies, with no mountain ranges or large bodies of water to serve as a barrier, was apparently sufficient that no subdivisions could be detected using DNA fingerprints from Swainson's Hawks in 85 nests from Manitoba to Alberta (Portman 1997). It appears, therefore, that our hawks were part of an interacting metapopulation semi-isolated only through the species' characteristic natal and breeding site fidelity. We suspect that the Saskatchewan and Alberta (Hanna) study areas were a source and a sink, respectively (Pulliam 1988). The source population may be indicative of emigration in a declining population.

In sharp contrast, a mountain range is apparently a barrier to dispersal for the population studied in the Butte Valley of northern California. The Butte Valley breeding population increased incrementally from 12 pairs in 1984 to 83 pairs in 1994 (a density of 20 territories per 100 km^2) and exhibited a high proportion of local recruits, while floaters or subadults were rare (Woodbridge et al. 1995).

Hawk population dynamics

In the Alberta (Hanna) study, a 69% increase occurred between pre-1986 and the three years of high population, 1986–1988. During these three years Swainson's Hawks responded quickly to the excellent food availability, the number of breeders increased, and both banded and unbanded non-breeders were common. Judging from the hawks' quick response, they were able to judge the suitability of an area with little delay, exemplifying Fretwell and Lucas's (1970) "ideal distribution." This response may have been mediated through the presence of a surplus of potential breeders that could saturate those nesting areas made newly available through an increase in food. The stabilizing influence of dispersal on population rate of change has been recognized in several studies (Hunter 1995). From 1986 through 1988, then, there was a surplus of Swainson's Hawks capable of breeding. It is unlikely that resident breeding hawks merely redistributed themselves from immediately outside the study area, because a regional (74 686 km^2) popula-

TABLE 4. Numbers of Swainson's Hawk nests and reproduction are shown for all SW Saskatchewan nests combined, and separately for a cereal and pulse crop production area near Kindersley and a mixed farming/ranching area near Alsask, east of the Alberta/Saskatchewan boundary.

	SW Saskatchewan			Kindersley			Alsask		
		Brood		Nests			Nests		
Year	Successful Nests	Size	S.D.	All	Failed	Brood Size	All	Failed	Brood Size
1944-1967	30	2.30	0.65						
1968	9	2.44	0.52						
1969	24	2.67	0.69						
1970	16	2.50	0.83						
1971	18	2.06	0.86						
1972	60	2.43	0.75	2	1	2.00			
1973	27	1.93	0.77	5	2	2.20			
1974	34	2.41	0.71	6	3	2.33			
1975	23	1.91	0.72	6	5	2.17			
1976	8	2.38	0.53	1	1	3.00			
1977	40	2.10	0.73	10	5	2.50			
1978	43	2.35	0.91	14	3	2.93			
1979	43	2.26	0.74	15	4	2.53			
1980	50	2.02	0.71	9	6	2.11			
1981	68	2.10	0.75	17	3	1.94			
1982	62	1.85	0.76	24	2	2.08			
1983	84	2.05	0.87	32	15	1.84			
1984	61	1.74	0.68	20	15	1.80			
1985	66	2.05	0.83	32	6	2.09	8	1	2.00
1986	113	2.08	0.78	38	3	2.13	13	6	1.85
1987	115	1.83	1.00	49	13	1.63	21	2	2.57
1988	97	1.68	0.76	18	19	1.50	26	8	2.08
1989	75	1.61	0.68	28	20	1.50	16	9	1.75
1990	113	1.70	0.74	34	13	1.47	16	8	2.06
1991	86	1.53	0.65	24	17	1.17	20	9	1.80
1992	91	1.59	0.65	29	18	1.38	6	14	1.67
1993	45	1.27	0.62	9	14	1.22	8	6	1.00
1994	95	1.83	0.81	25	1	1.88	6	11	1.50
1995	81	1.49	0.62	30	5	1.40	10	4	1.60
1996	50	1.48	0.71	16	12	1.69	7	5	1.14
Total	1727	1.92		493	206	1.80	157	83	1.89

tion estimate also showed an increase from an estimated 3879 nests in 1982 (Schmutz 1984) to 7 305 nests in 1987 (Schmutz 1989). Ferruginous Hawks responded similarly during these periods (Schmutz 1989). It is likely that at least in the moderate- and high-density years, the Hanna population had saturated all or nearly all available territories. The observation that the numbers of breeders within each of the three periods exhibited little variation in numbers is consistent with the notion of saturation at each level of prey availability. High nesting densities in comparison to other studies, regular nest spacing (Schmutz et al. 1980), and frequent aerial attacks observed throughout this study further support this conclusion. The juxtaposition of stability and change in long-term hawk dynamics is striking.

Near Hanna, reproduction in successful nests appeared stable through 1990 and then declined by 31%, followed by a hawk population drop in 1995 and 1996. In Saskatchewan, reproduction began to decline in 1988 (when Hanna numbers had peaked) and reached unprecedented low levels in 1993 and 1996, followed by a noticeable drop in hawk populations beginning in 1994.

Prey

Alberta (Hanna): In 1986, there was a close correspondence between the rise in hawk and ground squirrel numbers (Figure 2). The hawk population dropped near Hanna, the area where habitat had been altered least, only in 1995–1996 (Figure 2), four years after the drop in brood size (Figure 6).

Saskatchewan: Drastic ground squirrel prey and hawk brood size declines in Saskatchewan began in 1988 in the highly cultivated landscapes near Kindersley, Saskatchewan (Figure 3), earlier than in the rangelands near Hanna, Alberta. Alsask was intermediate in vegetation (Figure 1), and in timing of the

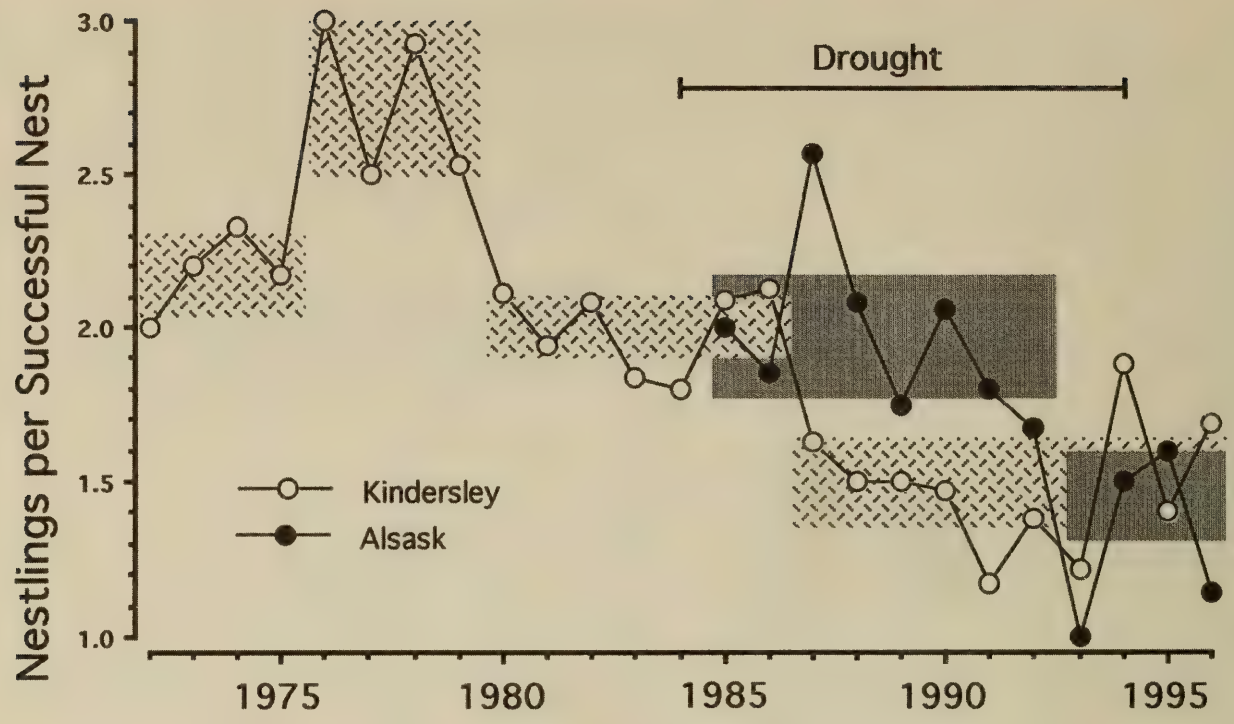

FIGURE 7. Annual mean number of nestlings reared by Swainson's Hawks in two regions of Saskatchewan. The drought period reflects below average annual precipitation on a plot showing a 10-year moving average.

declines. Record-setting heat during early June 1988, with accompanying drought and extensive loss of native vegetation at temporary ponds, may have contributed to the hawk brood size and ground squirrel declines. In Saskatchewan, brood size declines were followed six years later, in 1993, by the first sharp drop in nesting pairs. Some ponds were permanently drained and then cultivated. Pond loss is a widespread phenomenon on the prairies (Ignatiuk and Duncan 1995).

Food niche

On the Northern Great Plains, Swainson's Hawks have a two-niche feeding strategy. Adults feed mainly mammals to their young. But adults and fledglings rely heavily on insects, which are at their numerical peak after the young hawks have fledged.

The Hanna study area experienced high densities of grasshoppers that overlapped with the high in ground squirrels. In the Hanna study, perhaps a quarter of the breeding adults captured during the nestling stage had "dirty feet," as though they had been walking and feeding in fields, as non-breeding, insect-eating flocks are prone to do.

Based on over 1500 habitat-stratified sampling sites about 10 km apart in south-central and southeastern Alberta, Johnson and Worobec (1988) described 1978 to 1982 as years of low grasshopper density followed by "severe" outbreaks from 1983 to 1986. Computer-generated maps showed Hanna area grasshopper densities of 0–2 (1982), 2–4 (1983), 4–6 (1984), 4–6 (1985), and 2–4 (1986) grasshoppers/m^2, not quite reaching the 6–10/m^2 that defines a severe infestation. The most common species of grasshopper were *Melanoplus* sp. and *Camnula pellucida*.

Among eight studies reviewed by England et al. (1997), the percent of insects by items (not by mass) in the diet of Swainson's Hawks ranged from 0 to 55%. Only in New Mexico did insects comprise more than 20% of items; there, pellets were collected from nests and also on the ground (some of these pellets may have been shed by parent Swainson's Hawks, increasing the apparent insect representation in the diet). Given the largely vertebrate complement of other prey, these insects would comprise much less than 10% of biomass. No Swainson's Hawk population has been known to raise its nestlings on insects.

Therefore, the availability of grasshoppers and other insects may influence the dispersal of non-breeding hawks. The grasshoppers may have facilitated the increase by attracting non-breeders, which then filled new territories that became available during the peak three years of ground squirrel populations. Where insect and vertebrate availability coincide, breeding sites may be saturated and fledgling survival high, giving rise to a "source" population.

Food habits after fledging may differ from patterns reported during the nestling period. One road-killed fledgling found near Alsask in August 1975 had a crop engorged with insects. This reliance on insects results in part because adult male ground squirrels go into hibernation in June and adult females in July, leaving above ground only juveniles, whose numbers are reduced by predation (Yeaton 1972; Schmutz et al. 1979). Potential song-

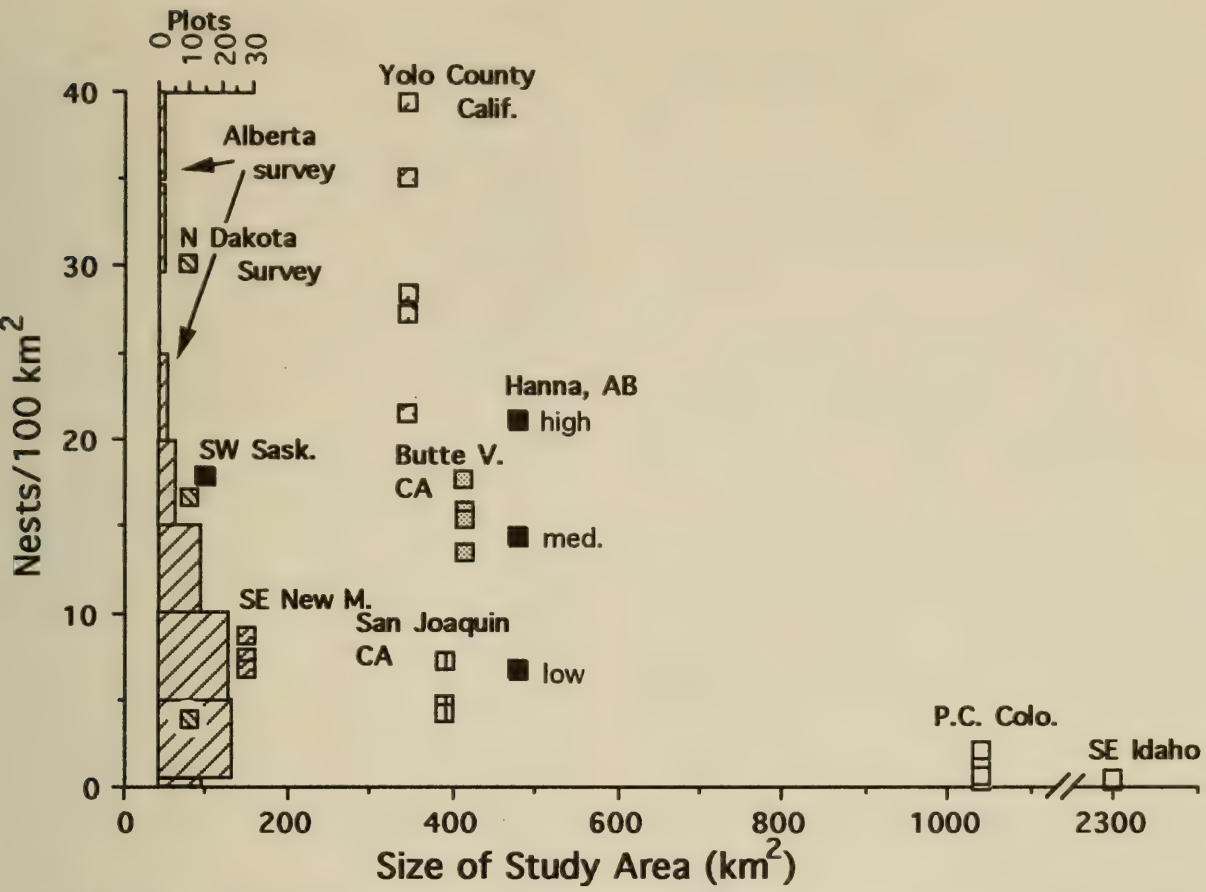

FIGURE 8. Swainson's Hawk densities based on study area size at Hanna (high, medium and low, Table 2), on the 1992 41-km^2 survey plots in SE Alberta (mean = 7.7 nests/100 km^2), and on a township in the Kindersley, Saskatchewan area are compared to other recent studies: North Dakota (3 years; Igl and Johnson 1997), Pinion Canyon, Colorado (4 years; Anderson 1995; SE New Mexico (3 years; Bednarz 1988; SE Idaho (3 years; Hansen and Flake 1995); Yolo County (5 years) and San Joaquin Valley (3 years), California, England et al. 1995; Butte Valley, California, (4 years; Woodbridge et al. 1995).

bird prey are now mature and some already have departed during the dry late summer. Insects, in contrast, are at their peak in August.

Hawk densities

In comparison with other parts of the species' range (southeastern Idaho, Hansen and Flake, 1995; southeastern Colorado, Andersen 1995; southeastern New Mexico, Bednarz 1988; Butte Valley, California, Woodbridge et al. 1995; Yolo Valley and San Joaquin Valley, California, England et al. 1995), our hawk densities are only slightly higher than average (Figure 8). The southeastern Alberta survey and that of Igl et al. (1999) in North Dakota may be the only studies where Swainson's Hawk population totals can be reliably extrapolated from samples representing 4.4% and 0.05%, respectively, of these two large regions.

Swainson's Hawks have adjusted remarkably well to cereal crop production, especially where a moderate mix of habitat persists. Our earlier analyses showed that Swainson's Hawk densities are higher on plots with >30% cultivation than on plots with 0-30% cultivation (Schmutz 1989). Elsewhere, nesting densities tend to be "...highest in areas with either a mixture of native habitat and agriculture or a high diversity of irrigated crops" (England et al. 1997).

Trees

Swainson's Hawks require trees or shrubs for nesting. Throughout previous centuries, almost annual range fires kept the prairies almost treeless. Apart from willows on the edges of sloughs, both study sites were virtually devoid of trees until settlers brought most fires under control about 1910 (Houston and Bechard 1983; Houston and Schmutz 1999).

The last major fire that burned over parts or all of the Hanna study area, eastward to near Alsask, occurred in 1909 (Gordon 1978). A much smaller fire there in 1978 burned some aspen clumps used by Swainson's Hawks, but the trees resprouted and supported Swainson's Hawks again by 1985.

Most farmers planted large shelter-belts, the trees supplied free from the Forest Nursery Station at Indian Head, Saskatchewan, founded in 1901 and by 1929 supplying four million trees per year (Cram 1984). Trees suitable for nesting by Swainson's Hawks became more accessible about 1950 as increasing numbers of farms were abandoned.

Although many of these planted trees have been plowed down, and others are deteriorating from neglect, trees remain more numerous than they were when European settlement began roughly 100 years ago. For this reason alone, Swainson's Hawks may now be more common on the northern Great Plains than they were in pre-settlement time.

A feature of Swainson's Hawk nesting ecology is the frequent use of low shrubs such as Willows, Chokecherry, Saskatoon, Buffaloberry, and Prickly Rose (Schmutz et al. 1980; Table 2), even when other trees are also available. Nest construction is well matched to a shrub nest base. Swainson's Hawks, unlike sympatric congeners, use herbaceous plants and small branching twigs (Schmutz et al. 1980), easily anchored among willow stems, though not always secured for long. This nest adaptability of Swainson's Hawks may reflect past selection pressures on tree-scarce plains.

Shooting of any hawk on sight, common in the early days of settlement by Europeans, is now rare; some pairs have proved adaptable enough to nest in occupied farmsteads. Since the 1940s, many more pairs have been able to use trees in deserted farmsteads although the remaining trees are untended, rubbed by cattle, sprayed with aerial herbicides, and damaged by drought. Each year, fewer of these former farmstead trees remain.

Agricultural effects

The "industrialization of agriculture" throughout most of the Great Plains has resulted in a reduced number of farms (Houston and Schmutz 1999), coincident with increasing use of fertilizer, pesticides, and herbicides; employment of larger machinery; bulldozing of abandoned shelterbelts; advent of rock-picking machines to allow breaking of marginal land; drainage of wetlands; cultivation of former railway rights-of-way and of the previous grassed and fenced 20.1 m wide road allowances, and use of chemical, untilled summer-fallow. Large areas of resulting treeless monocultures become unattractive to hawks and their prey species alike.

The future of the Swainson's Hawk rests largely with private ranchers and managers of government pastures. Ranchers, after all, are the stewards of the remaining grasslands. The Prairie Conservation Action Plan, launched in January 1986 at the first Endangered Species Workshop in Edmonton Alberta (Dyson 1996; Hummel 1987), is a promising development. More recently, the Saskatchewan Stockgrowers Association (SGA) has led the Prairie Conservation Action Plan Initiative. On 4-10 June 2000, assisted by other agencies and Saskatchewan Minister of Environment and Resource Management Buckley Belanger, the SGA proclaimed Native Prairie Appreciation Week.

Something deleterious is happening to grasslands, yet there is little evidence to suggest which changes in farming practice, alone or in combination, are responsible. With each decade the ever-smaller remnants of native habitat become an ever-scarcer component of the mosaic. It seems ironic that while the recent "industrialization/monoculturization" of agriculture is concentrated mainly on croplands, not grasslands, the continuing and seemingly inexorable bird species population declines affect grasslands disproportionately. Swainson's Hawk productivity studies offer one measure of change in the grassland-cropland ecosystem; increased understanding may in future guide us to more appropriate management techniques.

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APPENDIX 1. Prey items found in nests of Swainson's Hawks by region. The time period for the Saskatechewan study is split to allow comparisons between study areas. The number of items and their percentage by number and weight are reported. For prey near Hanna prior to 1983, see Schmutz et al. (1980).

	Saskatchewan								
	1966–1982			1983–1996			Alberta 1983–1996		
	#	%#	%Wt	#	%#	%Wt	#	%#	%Wt
Salamander									
Ambystoma tigrinum	1	<1	<1	1	<1	<1	5	1	<1
Leopard Frog									
Rana pipiens	1	<1	<1						
Plains Garter Snake									
Thamnophis radix	1	<1	<1	1	<1	<1	2	1	<1
Total Birds	**56**	**23**	**13**	**155**	**40**	**30**	**60**	**17**	**17**
Horned Grebe									
Podiceps auritus				1	<1	<1			
American Widgeon									
Anas americana, downy	4	2	<1						
Mallard *Anas*									
platyrhynchos, downy	4	2	<1						
Blue-winged Teal									
Anas discors, adult	1	<1	1	1	<1	1			
downy	3	1	<1	7	2	<1			
Northern Pintail									
Anas acuta, downy				1	<1	<1			
Lesser Scaup									
Aythya affinis, adult				2	1	2			
Unidentified duck, Adult	1	<1	1				5	1	3
Unidentified duck, Juvenile							5	1	<1
Swainson's Hawk, nestling	3	1	1	19	5	5			
Gray Partridge									
Perdix perdix				3	1	2	5	1	2
Sharptailed Grouse									
Tympanuchus phasianellus	2	1	3	5	1	5	5	1	5
Sora *Porzana carolina*	2	1	<1						
American Coot									
Fulica americana	4	2	4	6	2	5			
Total shorebirds	5	2	<1	11	3	1	8	3	2
Killdeer									
Charadrius vociferus	1	<1	<1	3	1	<1	1	<1	<1
Lesser Yellowlegs									
Trianga flavipes				1	<1	<1			
Willet									
Cataptrophorus semipalmatus				2	1	<1			
Spotted Sandpiper									
Actitis macularia				1	<1	<1			
Upland Sandpiper									
Bartramia longicauda	1	<1	<1	3	1	<1			
Long-billed Curlew									
Numenius americanus	1	<1	<1						
Marbled Godwit									
Limosa fedoa	1	<1	<1						
Baird's Sandpiper									
Speotyto cunicularia				2	1	<1			
Wilson's Phalarope									
Phalaropus tricolor	1	<1	<1						
Unidentified shorebird							7	2	1
Franklin's Gull									
Larus pipixcan	7	3	3	1	<1	<1			
Ring-billed Gull									
Larus delawarensis				1	<1	1			
California Gull									
Larus californicus				1	<1	1			
Unidentified gull							1	<1	<1
Burrowing Owl									
Calidris bairdii				1	<1	<1			

(Continued)

APPENDIX 1. *Continued.*

	Saskatchewan								
	1966–1982			1983–1996			Alberta 1983–1996		
	#	%#	%Wt	#	%#	%Wt	#	%#	%Wt
Total songbirds	20	8	6	96	25	8	35	10	4
Black-billed Magpie *Pica pica*	1	<1	<1	3	1	1			
American Crow *Corvus brachyrhynchos*	6	2	4	4	1	2	2	1	1
Horned Lark *Eremophila alpestris*	6	2	<1	52	14	3			
Vesper Sparrow *Pooecetes gramineus*	1	<1	<1	7	2	<1			
Lark Sparrow *Chondestes grammacus*				1	<1	<1			
Lark Bunting *Calamospiza melanocoris*				1	<1	<1			
Savannah Sparrow *Passerculus sandwichenis*	1	<1	<1	1	<1	<1			
Le Conte's Sparrow *Ammodramus lecontii*	1	<1	<1						
Chestnut-collared Longspur *Calcarius ornatus*				9	2	<1			
Unidentified sparrow				1	<1	<1	28	8	1
Bobolink *Dolichonyx oryzivorus*	1	<1	<1						
Red-winged Blackbird *Agelaius phoenicus*				2	1	<1			
Western Meadowlark *Sturnella neglecta*	2	1	<1	12	3	1	5	1	1
Brewer's Blackbird *Euphagus cyanocephalus*				1	<1	<1			
Brown-headed Cowbird *Molothrus ater*				2	1	<1			
House Sparrow *Passer domesticus*	1	<1	<1						
Unidentified bird							4	1	1
Total mammals	**187**	**74**	**81**	**228**	**59**	**70**	**272**	**78**	**70**
Shrew Soricidae				2	1	<1			
Nuttall's Cottontail *Sylvilagus nuttallii*				1	<1	1	1	<1	1
White-tailed Jackrabbit *Lepus townsendi*	6	2	21	9	2	24	6	2	14
Richardson's Ground Squirrel *Spermophilus richardsonii*	123	50	57	111	29	39	208	60	66
Thirteen-lined Ground Squirrel *Spermophilus tridecemlineatus*	3	1	1	2	1	<1	2	1	<1
Northern Pocket Gopher *Thomomys talpoides*	1	<1	<1	8	2	1			
Deer Mouse *Peromyscus* sp.	18	7	1	44	11	1	3	1	<1
Gapper's Red-backed Vole *Clethrionomys gapperi*	1	<1	<1	5	1	<1			
Meadow Vole *Microtus* sp.	34	14	1	41	11	1	46	13	1
Sagebrush Vole *Lagurus curtatus*							3	1	<1
Muskrat *Ondatra zibethicus*							1	<1	1
Norway Rat *Rattus norvegicus*				5	1	2			
Weasel *Mustela* sp.	1	<1	<1				2	1	<1
Total items	**246**			**385**			**349**		

Use of Host-mimicking Trap Catches to Determine which Parasitic Flies Attack Reindeer, *Rangifer tarandus*, Under Different Climatic Conditions

JOHN R. ANDERSON[1]*, ARNE C. NILSSEN[2] and WILLY HEMMINGSEN[3]

[1]Division of Insect Biology, University of California, Berkeley, California 94720 U.S.A. (jranderson@coinet.com)
[2]Zoology Department, Tromsø Museum, University of Tromsø, N-9037, Tromsø, Norway (arnec@imv.uit.no)
[3]Institute of Biology, University of Tromsø, N-9037, Norway (willyh@ibg.uit.no)

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Baited insect flight traps operated in subarctic Norway functioned as Reindeer mimics in capturing parasitic Oestridae and hematophagous females of four species of Culicidae, six of Simuliidae, seven of Tabanidae, plus unidentified Ceratopogonidae. CO_2-baited traps caught significantly more flies in the above taxa than non-baited traps. There was no significant difference in catches of these flies between traps baited with CO_2 and CO_2 plus Reindeer interdigital pheromone glands (IDPGs), but both types of CO_2-baited traps caught significantly more culicids and simuliids than traps baited only with Reindeer IDPGs. No tabanids were caught in traps baited only with Reindeer IDPGs. CO_2-baited traps caught large numbers of culicids and simuliids on cool, overcast days (when few or no oestrids were caught). On warm, sunny days (when most oestrids were caught) the largest numbers of culicids and simuliids were caught during the crepuscular/night-time period. Overnight trapping and landing/swarming counts at humans revealed that small numbers of culicids remained active throughout the night time hours at 7°C, or higher. Wind speeds of 8-10 m/s negated or greatly depressed catches of all hematophagous flies in stationary traps. Binocular observations of Reindeer and analysis of videotaped Reindeer movements revealed anti-fly behavioral reactions to tabanids at one study area. The most severe anti-fly reactions occurred on warm (17-25°C), sunny days (when the largest numbers of oestrids were trapped and seen around herds). However, even on the few favorable days for oestrid activity, Reindeer had an overnight period of 6-10 hours during which the small numbers of culicids active then did not interfere with foraging.

Key Words: Reindeer, *Rangifer tarandus*, CO_2-baited trap catches, parasitic fly harassment, anti-fly behavior, foraging behavior.

Although there are many reports of insects harassing Caribou/Reindeer (*Rangifer tarandus*), there are almost no data concerning the guild of parasitic flies associated with these animals in different geographical areas (Anderson and Nilssen 1998), nor on the relative abundance/importance of the various parasitic fly species that attack these hosts. Most reports about parasitic flies associated with these animals mention only mosquitoes (*Aedes* spp.), the Reindeer Warble Fly, *Hypoderma tarandi*, and the Nasopharyngeal Bot Fly, *Cephenemyia trompe*. Only Bergman (1915), Breev (1950) Low (1976) and Helle et al. (1992) have provided data for hematophagous species caught attacking Caribou/Reindeer. In Sweden, Bergman (1915) reported four species of Tabanidae, three species of Culicidae, two species of Ceratopogonidae and two species of Simuliidae collected from tame Reindeer. In collections from tame Reindeer in USSR, Breev (1950) reported 15 species of Tabanidae, 10 species of Simuliidae and six species of Culicidae, but specimens identified from aliquot samples included only three species of Tabanidae, two species of Culicidae and two species of Simuliidae. In samples from two recently dead Woodland Caribou in British Columbia, Canada, Low (1976) reported collecting a "few" specimens of *Simulium* species and *Tabanus* species, "many" *Aedes pionips*, "moderate numbers" of unidentified culicids and a "few" ceratopogonids. More recently, Helle et al. (1992) collected seven species of Tabanidae, three species of Simuliidae, and one species of Ceratopogonidae from a tame Reindeer, and Anderson and Nilssen (1998) collected and observed one culicid species and one tabanid species from Reindeer, and caught three other culicid species and six simuliid species in host-mimicking traps. We also observed a muscoid fly (*Hydrotaea* species) around the eyes and wounds of a tame Reindeer (unpublished data).

As with our studies of Reindeer oestrids (Anderson and Nilssen 1996a), the primary objectives of this study were to compare the response of parasitic hematophagous flies to CO_2-baited and unbaited traps, and to traps baited with CO_2, CO_2 plus Reindeer interdigital pheromone glands (IDPGs), and with only Reindeer IDPGs. Other objectives were to compare catches of hematophagous flies in traps

*Corresponding author

operated in a birch/willow woods, in treeless vidda habitat, and along the woods:vidda ecotone; determine the numbers of flies caught at different times of the day; observe Reindeer for anti-fly behaviors; and determine culicid densities around humans. After the first year of trapping revealed that many hematophagous flies had not entered the apical collecting container of a trap at the time a trap was shut down, a final objective was to determine the percentage of such flies caught in traps that were in the apical collection container versus the percentage caught in the main body of the trap. Trap catch data were used to reveal which parasitic flies were most abundant on days Reindeer were observed exhibiting anti-fly behavioral reactions.

Materials and methods

Study areas

Studies were conducted in Finnmark and Troms counties in northern Norway, 340–360 km north of the Arctic Circle. At study area "A" (Vaddas, 69° 50′N, 20° 40′E, altitude 140–160 m) and "B" (Suolovuopmi, 69° 37′N, 23° 31′E, altitude 440–520 m) the typical mountainous Reindeer habitat consists of an upper permafrost-free vidda (=tundra) biome interspersed with numerous rivers, streams and lakes and characterized by vegetation such as Dwarf Birch (*Betula nana*), Bilberry (*Vaccinium myrtillus*), Cloud Berry (*Rubus chamaemorus*), sedge (*Carex* spp.) tussocks, mosses (Bryophyta), and lichens (Mycophycophyta). Below about 500 m there are wooded hillsides and valleys and, generally, larger streams and rivers. The predominant trees in wooded areas are Mountain Birch (*Betula pubescens tortuosa*) and willows (*Salix glauca* and *S. lapponum*), with an under layer of Dwarf Birch and Juniper (*Juniper communis*).

Traps and baits used

Parasitic flies were collected in the type of insect flight trap shown in Figure 1 and described in more detail in Anderson and Nilssen (1996a). Baited traps received 4–6 kg of dry ice placed in a styrofoam box set at the base of a trap's center support pole and, in one experiment, traps also were baited with CO_2 plus two IDPGs and IDPG-treated cords (Anderson and Nilssen 1996a). Sublimated CO_2 escaped through a hole near the bottom of each side of the styrofoam box. CO_2 emission rates of 1.5–2.5 l/min were determined by periodically weighing dry ice baited boxes.

In 1984, traps at area "A" were operated on 12 of 20 on-site days between 14 June and 27 July, and at area "B" on 11 of 14 on-site days between 30 July and 17 August. In 1985, traps at area "B" were operated on 28 of 39 days between 23 July and 31 August, and in 1987 they were operated on 14 of 28 days between 20 July and 17 August.

FIGURE 1. Insect flight trap with styrofoam box containing dry ice set at the base of center support pole and apical collecting container mounted in place.

Collection and handling of flies

When traps were shut down, most trapped culicids and simuliids were resting on the lower trap panels and within the upper canopy. Therefore, on all except four days recorded trap catches of these flies consisted only of the numbers in each trap's apically-situated collecting container, which was removed and plugged with cotton. After removal of oestrids, the containers were stored in a deep freeze unit until processed. On four days, we determined the total number of flies caught in each trap at the time it was shut down. This was done by first using a battery-powered aspirator (Meyer et al. 1983) to collect all flies resting on inner trap panels and inside the upper canopy of a trap. After aspirating all flies from the main body of a trap, the apical collecting container was removed, sealed and replaced with an empty container. As traps were shut down, we collected an aspirator sample from 22 traps; each aspirator sample was paired with a corresponding collecting container sample. These samples (collected between 17:00 and 20:30 h) were taken to address our final objective. Each sample was placed in a sealed polyethylene bag, and frozen in a dry ice box. The power aspirator also was used to collect flies from a Reindeer calf on one day, and on another day it was used to collect flies attracted to a CO_2-baited Reindeer model (illustrated in Anderson and Nilssen 1990). Trapped specimens were identified to family level and counted, and representative specimens were pinned or preserved in 70% ethanol for later specific identifications. Species collected from the Reindeer calf and CO_2-baited Reindeer model were compared with trap catches.

Experimental Designs

At study area "A" four baited traps in birch/willow woods habitat were sited in zig-zag fashion about 100 m apart; trap sites increased from 140 m to 150 m in elevation. Trap 4 was 100 m from the woods:vidda interface. In vidda habitat, two to four traps were sited 100–200 m apart at elevations of 350 m to 450 m. When climatic conditions permitted, traps were operated from about 09:00 to 22:00 h, and on four days, catches were separated into two trapping periods (09:00–15:00 h and 15:00–22:00 h); all times throughout are provided in Norwegian Standard Time (NST).

At study area "B", we operated a baited trap at each of four sites in birch/willow woods habitat (elevation 440–450 m) (Figure 1) and at four to eight sites in treeless vidda habitat (elevation 500–520 m). In 1985, we also operated traps at four sites along the north edge of the woods:vidda interface. As described in greater detail in Anderson and Nilssen (1996a), woods traps were set at the corners of a square measuring 250 m on a side, vidda traps were linearly spaced at 400–600 m apart, and edge traps linearly spaced at about 500 m apart. The maximum distance between traps (first woodland and last vidda) was 4.25 km.

The responses of hematophagous flies to CO_2 were determined from paired CO_2-baited and unbaited control traps placed at six woodland sites on eight days. The responses to CO_2, CO_2 plus two IDPGs and gland-treated cords, and IDPGs and gland-treated cords only, were determined by operating one trap with each bait at each of four woodland sites on three days (12 replicates of each treatment). For each baited trap experiment, traps were sited 25–50 m apart in a small woodland clearing, and perpendicular to the prevailing wind. To assess nocturnal activity, baited traps were operated at woods and vidda sites from about 19:00 to 08:00 h the following morning on eleven dates between mid-July and mid-August.

Beginning in August 1984, and in 1985, traps usually were started from 09:30 to 10:30 h and shut down from 18:30 to 19:30 h (as climatic conditions permitted). In 1987, traps were shut down from 16:00 to 21:00 h (Table 4). At first trap start up time, about mid-day and at last trap shut down time we recorded percentage cloud cover, temperature, light intensity and wind direction and velocity. On most days in 1984 and 1985 the above schedules did not permit trapping through the times when culicids and simuliids were at peak attacking densities (from about 17:00 to 20:00 h). Given the expense and limited quantity of dry ice, and our primary focus on oestrids in 1984 and 1985 (Anderson and Nilssen 1996a,b), we opted to conserve dry ice for a maximum number of oestrid trapping days (oestrid activity after 19:00 h was rare) (Anderson and Nilssen 1996a).

Reindeer Observations

As traps were operating, groups of Reindeer were intermittently observed with binoculars (1984, 1985) or videotaped (1987) whenever they were located. Such Reindeer usually were found from 5–15 km from traps. Whenever possible individual animals among groups of 2–20 were observed for 5-minute periods; larger groups were scanned for 5 minutes. In wooded areas, most animals were observed for only 1–2 minutes before they moved out of sight. Videotapes were analyzed for herd movements and for defensive, anti-fly behaviors by yearlings and adults. On three days in 1984, we observed a tame, dark brown, 3-year old cow from distances of 0.5 to 10.0 m as she reacted to hematophagous flies.

Culicid attack indices at humans

Mosquito densities at humans were assessed by estimating the number attracted to a stationary person who had walked for 50–100 m into a birch/willow forest or onto the treeless vidda. The estimated attack indices included the resting/probing mosquitoes located from the knees to the top of the head, plus those swarming in the same area. The attack indices used were: I=1–10; II=11–25;

III=26–40; IV=41–100+. Human attire consisted of tan or blue clothing and caps. Because many mosquitoes were present in a hovering/following swarm (which sometimes also included simuliids), on several occasions we also used an insect net (30.5 cm dia.) to make 10 figure 8 sweeps from knee level to a point about 0.5 m overhead while slowly circling counterclockwise. After waiting for a minute while the disrupted swarm moved in again, the sweeping procedure was repeated once.

Statistical analysis

Catches of flies in traps baited with CO_2 versus non-baited control traps were analyzed with a two-way ANOVA with date as cofactor. Catches of flies in traps baited with CO_2, CO_2 + IDPGs, and IDPGs only were analyzed with a two-way ANOVA with date as cofactor; effect of bait was tested with HSD Tukey post hoc tests. Fly catches in CO_2-baited traps operated in 1985 at woods, vidda, and ecotone edge sites were subjected to a fully factorial two-way ANOVA (date and habitat as factors), to evaluate the effect of habitat on the number of culicids and simuliids caught. The 1984 catches of tabanids at woods and vidda sites were analyzed with a one-way ANOVA. In all ANOVAs, catches were log10 (X + 1) transformed before the analyses to eliminate dependence of the variance upon the mean and to aid additivity. A paired sample t-test was used to test for significant differences in numbers caught during the first versus the second period of trapping. A correlation analysis on catch data was used to statistically evaluate relationships among the numbers of flies caught on different days. The resulting correlation matrix was used to produce a multidimensional scaling plot illustrating the correlations. All statistical tests were carried out using SYSTAT 5.2 (SYSTAT 1992).

Results

Response of hematophagous flies to baited and unbaited traps

Except for 38 male tabanids and 18 male simuliids caught during three summers, both baited and unbaited traps caught only female flies. In addition to the four species of Culicidae and six species of Simuliidae previously reported being caught in our CO_2-baited traps (Anderson and Nilssen 1998), such traps caught females of the following species of Tabanidae: *Chrysops nigripes*, *Haematopota pluvialis*, *Hybomitra auripila*, *Hy. lundbecki*, *Hy. montana*, *Hy. nitidifrons confiformis*, *Hy. sexfasciata*, and an unidentified *Hybomitra* species. The CO_2-baited traps also caught species of Ceratopogonidae, but these were not identified and tallied.

Catches of culicids, simuliids and tabanids in CO_2-baited insect flight traps (respective means ± SD = 125.8 ± 31.8; 206.0 ± 31.9 and 1.67 ± 75) were significantly greater than those in paired, unbaited control traps (respective means ±SD = 9.27 ± 37.2; 7.18 ± 37.3 and 1.18 ± 0.88) (respective $P = 0.00001$, 0.00000002 and 0.028). There was no significant difference in catches of culicids between traps baited with CO_2 and CO_2 plus Reindeer IDPGs ($P = 0.43$). However, both types of CO_2-baited traps (3040 and 4217 females, respectively) caught significantly more Culicidae ($P = 0.00027$) than traps baited only with Reindeer IDPGs (422 females) ($P = 0.00014$). Both types of CO_2-baited traps (10350 and 9187 females, respectively) also caught significantly more Simuliidae ($P = 0.00018$) than traps baited only with Reindeer IDPGs (147 females) ($P = 0.00018$). For Tabanidae, traps baited with CO_2 and CO_2 plus Reindeer IDPGs caught only 15 females; no tabanids were caught in traps baited only with Reindeer IDPG.

Catches of flies in different habitats

Traps operated on the same six days in different habitats revealed that significantly fewer simuliids and tabanids were caught in traps set at vidda sites, than at woodland or edge sites, and that significantly fewer culicids were caught in traps set at edge sites (Table 1).

Tabanids trapped at study area "A"

At study area "A" in 1984 we caught many more tabanids at woodland sites than at vidda sites, and the diversity of species was greater at woodland sites (Table 2). Of the 5016 tabanids caught in woodland traps on the six days shown in Table 2, 4829 (96.27%) were *Hy. auripila*, 167 (3.33%) were *H. pluvialis*, and 20 (0.40%) were *C. nigripes*. All 498 tabanids caught in vidda traps on these six days were *Hy. auripila*.

On four days when trap catches at woodland sites were separated into catches from 09:00–15:00 h and 15:00–22:00 h, a paired sample t-test revealed that the first period mean of 113.8 ± 77.2 SD flies/trap was not significantly different from the second period mean of 102.1 ± 64.4 SD flies/trap ($t = 1.157$, df = 16, $P = 0.264$). However, for vidda trap catches on these days the first period mean of 30.0 ± 16.5 SD flies/trap was significantly different from the second period mean of 11.5 ± 10.3 SD flies/trap ($t = 3.52$, df = 11, $P = 0.00475$). When catches at woodland sites were compared with catches at vidda sites (Table 2) the data revealed that the woodland mean of 209.0 ± 121.2 SD flies/trap was significantly greater than the vidda mean of 42.3 ± 22.8 SD flies/trap ($F = 87.61$, $P < 0.0001$). In comparably-baited traps operated on the vidda in this same area in 1985, the mean number of tabanids/trap/day was 83.0 and in 1987, it was only 36.5 (Anderson and Nilssen 1998).

Tabanids trapped at study area "B"

Tabanids were caught in far fewer numbers at study area "B" than at study area "A" (Tables 3, 4). At study area "B" we caught the same three species caught at study area "A", plus: *Hy. lundbecki*, *Hy.*

TABLE 1. Mean ± SD number of hematophagous flies caught per trap collection container per day in CO_2-baited insect flight traps, 1985.*

Site	No. trap days	Culicids	Simuliids	Tabanids
Woods	27	68.9 ± 82.8a	198.0 ± 201.6a	3.2 ± 3.2a
Edge	24	34.3 ± 34.8b	113.7 ± 53.2a	2.4 ± 3.3ab
Vidda	12	77.6 ± 71.4a	69.8 ± 59.5b	0.75 ± 1.1b

*Mean numbers represent about 25% of total culicids caught in traps and about 50% of total simuliids caught in traps. Means followed by the same letter (within columns) are not significantly different (ANOVA, HSD Tukey test, $P > 0.05$). Two traps/day at vidda area, 4 traps/day at edge area and 4 traps/day at woods area (except 5 on 31 July and 6 on 2 August).

montana, *Hy. nitififrons confiformis* and *Hy. sexfasciata*. Tabanid populations at this inland site probably peaked before yearly trapping began.

Percentage of flies caught in apical collecting containers of traps versus numbers aspirated from interior panels and canopy of traps at shut down times

The 22 samples in which the number of flies in the apical collection containers was compared with the number aspirated from the inner panels and canopy of the trap revealed that, for culicids, about 1/4 (mean 22%, median 24%) of the catch was in the apical collecting container. For simuliids, about 1/2 (mean 42%, median 47%) of the catch was in the apical collecting container. On 2 and 8 August 1985, 76% of 21 tabanids caught in 14 traps were in the apical collecting containers, and on 21 and 30 July 1987, all of 4 tabanids caught in 8 traps were in the apical collecting containers.

Comparison of biting fly catches with oestrid catches on different days

Knowledge of the percentages of biting flies in collecting container samples allowed estimates of total numbers caught on all days for comparison with the total number of oestrids caught on different days. Such comparisons revealed that CO_2-baited traps caught large numbers of biting flies on days that were mostly unfavorable for oestrid host-seeking activity (Tables 3, 4). The correlation matrix (Table 5) and multidimensional scaling plot (Figure 2) show that the best catches of culicids and simuliids were positevely correlated, as were catches of the two oestrids. Similar comparisons for 1984 catches could not be made because almost all culicid and simuliid collections were destroyed in storage. In addition to the 1985 dates in Table 3, on 3 through 6 July 1985, six CO_2-baited traps operated at area "B" caught a mean of 117.3 ± 116.1 culicids and 23.3 ± 24.9 simuliids, but no oestrids or tabanids. After 10 August 1985 both the oestrid and biting fly populations declined severely. *Hypoderma tarandi* declined to 1.1/trap on 14 August and less than 0.5/trap thereafter; *C. trompe* remained at less than 0.5/trap after 10 August. In 10 traps, only one *H. tarandi* was caught on 18 August and one *C. trompe* on 21 August (Anderson and Nilssen 1996a). No oestrids were caught in 8 to 10 traps/day on 22 and 28 to 31 August.

After 10 August 1985 total culicid catches varied from 30–40/trap and simuliids from 40–50/trap through 22 August. Total culicid catches remained at 5–10/trap and simuliids from 10–20/trap through 30 August.

In addition to the eight days shown in Table 4, 12 CO_2-baited traps operated on 24 and 27 July were estimated to have as many culicids and simuliids per trap as were caught on 21 July, but all traps caught only one *C. trompe* and one *H. tarandi* on 24 July, and only one *H. tarandi* and three tabanids (*H. montana*) on 27 July.

Climatic conditions associated with trap catches of parasitic flies

Trapping days not included in Tables 3 and 4 experienced some combination of being darkly overcast, cool (7–14°C) and windy (8–10 m/s), or cool and rainy. Temperature, light intensity and wind velocity affected the host-seeking activity of all flies captured (Table 6, and Anderson and Nilssen 1996a, for 1985 climatic conditions). Most oestrids were caught on warm (17–25°C), mostly sunny and calm days. On 27 trapping days during three years oestrids were not

TABLE 2. Mean ±SD number of tabanids caught per trap collecting container per day, 1984.*

Date	Woods	Vidda
20 June	63 ± 39.0 (4)#	—
23 June	151 (1)	—
27 June	191.3 ± 49.9 (4)	—
9 July	189.4 ± 106.2 (5)	43 (1)
10 July	193.7 ± (3)	45.0 ± 29.1 (3)
12 July	395.3 ± 62.3 (4)	52.0 ± 31.5 (4)
24 July	222.5 ± 51.6 (4)	30.5 ± 5.4 (4)

*Numbers caught in apical collection container of a trap represent 76% of the total catch (aspirator samples on 4 days revealed that 24% of the tabanids in the trap were resting on inner surface of trap panels and the trap canopy).

#Number of traps. For 23 June, several collections were inadvertently destroyed in storage.

TABLE 3. Comparative ranking of best CO_2-baited trap catch days for culicids versus other taxa of parasitic flies, 1985*.

Date	Culicid rank	Simuliid rank	*H. tarandi* rank	*C. trompe* rank	Tabanid rank	Time of last collection
29 July	I (484)#	IV (266)	III (5.7)	IV (0.6)	I (5.9)	1720 h (17.1)+
9 August	II (297)	V (147)	V (3.9)	IV (0.6)	VI (0.8)	1730 h (14.0)
2 August	III (292)	I (530)	IV (4.1)	II (1.0)	III (2.3)	1921 h (15.3)
31 July	IV (136)	II (341)	VI (1.8)	V (0.5)	II (4.0)	1734 h (18.0)
8 August	V (61)	III (296)	I (11.5)	I (2.67)	V (1.3)	1830 h (14.8)
10 August	VI (21)	VI (83)	II (6.8)	III (0.9)	IV (1.6)	1836 h (19.0)

*Catches of flies are from 6-10 traps operated on different days at woodland, vidda and woodland:vidda edge sites.
#Mean number of flies/trap in parenthesis. For culicids, simuliids and tabanids mean numbers for 2 and 8 August are based on the actual trap totals (apical collection container catches plus flies aspirated from interior trap panels and trap canopy); mean numbers for all other dates are based on adjusted totals estimating that only 25% of all culicids, 50% of all simuliids, and 75% of all tabanids trapped were in apical collection containers.
+Temperature (°C) at time of last collection; Time (NST).

trapped when temperature was below 10°C; on dark, cloudy or rainy days (light intensity below 20 000 lux); or at wind velocities above 8 m/s. Most tabanids were caught on days having the same climatic conditions favoring oestrid activity, with only four caught on oestrid-negative days in 1985. Culicids and simuliids, however, were caught on all trapping days negative for oestrids and tabanids, as well as on the days shown in Tables 3 & 4. Culicids and simuliids were not trapped when the temperature was less than 7.0°C or when wind velocities were 8–10 m/s. On some days, warm, sunny conditions were favorable for host-seeking activity by oestrids, tabanids and biting flies (e.g. Table 3, 29 July & 2 August; Table 4, 4, 9–10 August). On such days (Table 7) culicid and simuliid numbers peaked during the crepuscular period.

Because of adverse climatic conditions while at field study sites traps were not operated on 11 days in 1984, 11 days in 1985 and 14 days in 1987. These days, plus the oestrid-negative trapping days, revealed that adverse climatic conditions prevented oestrid host-seeking activity on 21 of 35 days in 1984, 22 of 39 days in 1985, and 19 of 28 days in 1987.

Catches of hematophagous flies at different diel times

For trap catches collected twice a day in 1985 paired sample *t*-tests revealed that significantly fewer simuliids were caught in traps from 09:30 to 14:30 h than were caught in traps from 14:30 to 19:30 h ($t = 4.01$; df = 54; $P = 0.00019$), but no significant difference in the numbers of culicids caught during the first versus the second trapping period ($t = 0.97$; df = 54; $P = 0.34$) nor the numbers of tabanids caught during the first versus the second trapping period ($t = 0.026$; df = 54; $P = 0.98$).

Temperature during crepuscular/overnight trapping periods had a marked affect on the number of culicids caught. Both the largest and smallest numbers of culicids were caught when traps were operated from early crepuscular hours through an overnight period (Table 7).

At temperatures of 12.0°C to 14.0°C, large num-

TABLE. 4. Comparative ranking of best CO_2-baited trap catch days for culicids versus other taxa of parasitic flies, 1987*.

Date	Culicid rank	Simuliid rank	*H. tarandi* rank	*C. trompe* rank	Tabanid rank	Time of last collection
31 July	I (2034)#	I (2369)	VI (0.63)	IV (0.13)	V (1.0)	2100h (14.0)+
30 July	II (1768)	III (1118)	V (0.70)	V (0.10)	VI (0.0)	1932h (11.2)
21 July	III (497)	VII (214)	VII (0.50)	VI (0.0)	II (2.0)	1608h (13.6)
4 August	IV (493)	VI (499)	IV (0.75)	III (0.25)	V (1.0)	2015h (16.9)
10 August	V (381)	IV (756)	II (4.4)	II (0.22)	IV (1.3)	2000h (11.8)
9 August	VI (342)	II (1529)	I (6.2)	I (0.40)	III (1.8)	2030h (10.7)
6 August	VII (257)	VIII (200)	VIII (0.0)	VI (0.0)	VII (0.0)	2057h (10.0)
20 July	VIII (118)	V (621)	III (1.0)	VI (0.0)	I (10.5)	1733h (23.3)

*Catches of flies are from two traps operated at woodland sites on 20 and 21 July, and from 4-8 traps operated at woodland and woodland:vidda sites on all other dates.
#Mean number of flies/trap in parenthesis. For culicids and simuliids mean numbers for 21 and 30 July are based on total trap catches (apical collection container catches plus flies aspirated from interior panels and canopy of traps); mean numbers for all other dates are based on adjusted totals estimating that only 25% of all culicids, 50% of all simuliids, and 75% of all tabanids trapped were in apical collection containers.
+Temperature (°C) at time of last collection; Time (NST).

TABLE 5. Pearson correlation matrix (r-values) from a correlation analysis based on mean catch data of the taxa shown in Tables 3 and 4, both years combined.

	Culicidae	Simuliidae	*H. tarandi*	*C. trompe*	Tabanidae
Culicidae					
Simuliidae	0.76**				
H. tarandi	-0.43	-0.21			
C. trompe	-0.36	-0.27	0.87**		
Tabanidae	-0.31	-0.13	-0.05	-0.12	

**significant ($p < 0.001$)

bers of culicids (*A. communis*, *A. pionips* and *A. punctor*) were collected from 19:00–20:20 h in power aspirator samples taken on 10 August 1987 while slowly walking around a CO_2-baited Reindeer model and collecting flies landed on and swarming around the model (Table 8). For comparison with these numbers, the adjusted mean number of culicids caught/trap in nine traps set at similar woodland sites on this date was 381 (range = 296–624); for simuliids the number was 756/trap (range = 120 to 2904). The culicid index around a person in a woodland clearing was III at 19:00 h and IV at 20:00 h (see below) On the Reindeer model culicid and simuliid females crawled and probed areas of the head, as well as the Reindeer hide covering the body; *H. tarandi* females laid eggs on the hairs and *C. trompe* deposited larvae on the muzzle (Anderson and Nilssen 1990).

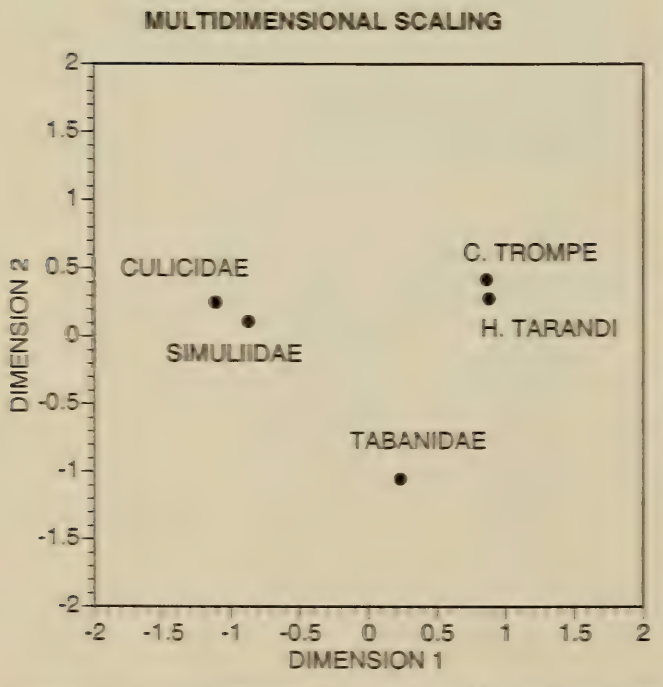

FIGURE 2. Multidimensional scaling (MDS) plot based on the correlation matrix in Table 5. Taxa close to one another show a positive correlation (abundance fluctuates mostly synchronously), whereas distant taxa show a high negative correlation.

Culicid swarming/landing indices at humans

The 1987 swarming/landing indices of mosquitoes attracted to a human who had walked 50-100 m into a birch woodland are shown in Figure 3. Vidda indices were similar, except that on 20 July and on 1 and 5 August, winds of 5.0–8.5 m/sec negated culicid attraction to humans throughout most of the day. Because of adverse climatic conditions on dates not shown, culicid activity was at the 0 to I level. The following swarm often included as many, or more, culicids than had landed on the observed human, as well as smaller numbers of simuliids. At a swarming/landing index of level IV on two dates, the mean catch of culicids in 20 figure 8 sweeps with an insect net was 59.5 ± 13.4; for level III on two dates the mean catch was 33.5 ± 2.3, and for level II on three dates the mean catch was 18.7 ± 6.5. In these collections, culicids comprised 77.5% of the catch and simuliids 22.5%. *Aedes communis*, *A. pionips* and *A. punctor* were caught biting, and in sweep net collections.

The number of attacking culicids fluctuated somewhat with time of day and temperature. If the temperature was above 10.0°C in the morning, attack rates were at level II or III from about 09:00 to 12:00 h. At temperatures between 10.0°C and 20.0°C numbers attacking nearly always were lowest (level I or II) between 12:00 and 15:00 h, but they usually increased to level III or IV between 16:00 and 20:00 h. After 19:00–20:00 h, culicid biting activity decreased with decreasing temperature. At 7–10.0°C, it was always at level I between 20:00 and 00:30 h. On five dates, no culicids were observed at temperatures of 3.5 to 5.5°C (times were 07:00–08:15, 22:20 and 24:00 h).

Simuliids attracted to humans

In both woodland and vidda habitat, simuliids also sporadically swarmed about humans, but as they rarely landed and attempted to bite, their numbers were not estimated. In 20 figure 8 insect net sweeps taken when the culicid swarming/landing index was at level IV, the mean ± SD catch of simuliids was 8.5 ± 7.8; at culicid level III the mean catch of simuliids was 16.0 ± 5.7, and at culicid level II the mean catch of simuliids was 8.0 ± 7.8.

Movements and reactions of Reindeer to flies

At study area "A" from 19 June through 24 July

TABLE 6. Climatic conditions associated with daytime catches of parasitic flies in Table 4*

Date	Percent cloud cover#	Temperature# min	mean	max	Wind velocity+ (m/s)
31 July	75.0	0.8	9.6	15.8	2.0–4.0/0.0-2.0
30 July	75.0	-0.6	8.5	14.2	3.0–4.5/1.0-2.0
21 July	100.0	8.2	14.6	22.6	3.0-5.0/2.0-2.5
4 August	37.5	8.4	15.8	21.0	3.0/0.5-2.0
10 August	37.5	0.2	10.8	18.2	1.5-2.5/0.0-1.1
9 August	12.5	-1.6	9.3	17.0	1.0-2.0/0.0-0.5
6 August	25.0	4.5	9.6	14.6	4.0-5.0/2.0-3.0
20 July	50.0	10.6	19.5	25.4	5.5-6.5/3.0–4.0

*Order of dates conforms to order of dates in Table 4.
#Cloud cover and temperature data are from the Norwegian weather station at Suolovuopmi, located 2.5 km from the center of the woodland trapping site at study area "B".
+Maximum velocities at different trap sites over minimum velocities.

1984. Reindeer moved out of woodland habitat and up onto the treeless vidda prior to 07:00–08:00 h. They moved back down into the woodland between 19:00 and 19:30 h. Groups of 50–100 animals observed on the vidda from 10:00 to 13:00 h on two warm, sunny days foraged at a moderate walking pace for about 5–10 minutes and then suddenly trotted for 50 to several hundred meters, after which they again began walking and foraging. Individual animals observed with binoculars reacted with the types of anti-fly behaviors described by Anderson and Nilssen (1998). These observations and trap catches (Table 2) indicated that the animals were reacting to tabanids.

Reindeer observed from 19:30 to 22:00 h (after tabanid activity had ceased) slowly walked and foraged through the woods. During 1–5 minute observation periods about half of these animals responded with one or two mild reactions consisting of a shaking leg kick, tail wag/ rump shake, ear flick, or a head shake. All such responses are typical of host reactions to culicids (Anderson and Nilssen 1998). The slow foraging pace through woodland, and mild anti-fly reactions, indicated little or no harassment by culicids.

A tame three-year-old cow attacked by culicids at study area "B" exhibited similar reactions as she walked, paused and foraged. When attacking numbers reached an estimated 40–50 culicids the cow responded with a head/body shake or body shake, and then trotted to a new foraging site and resumed feeding. Culicids were seen feeding around the eyes and on the muzzle, antlers, and legs, as well as crawling and probing on the body. A fortuitously encountered sick fawn sampled for attacking flies on 20 July 1987 remained lying motionless while attacked by hundreds of culicids. A 4-min power aspirator sample taken at 19:30 h (20°C) contained 468 culicids (*A. communis*, *A. pionips* and *A. punctor*) and one unidentified *Simulium* spp.

At study area "B", the foraging activity of Reindeer rarely appeared to be even moderately affected by parasitic flies (Table 9). One exception occurred on 9 and 10 August 1985 when 40-50 Reindeer were observed standing and lying on the highest mountain top in the area (639 m). At wind

TABLE 7. Effect of temperature on crepuscular/overnight catches of culicids*.

Date	Trapping hours	Number of traps	Temperature# (°C)	Number of culicids/trap+
13 July 1984	18:20 - 08:20	1	12.2/10.4	520
30 July 1984	18:10 - 07:50	1	16.0/7.4	2973
31 July 1984	18:35 - 08:15	4	17.2/6.5	1757 ± 388
2 July 1985	18:45 - 08:12	1	13.7/4.0	577
25 July 1985	17:45 - 08:15	1	18.0/12.0	400
9 July 1987	19:35 - 09:05	3	8.5/5.4	2.0 ± 1.15
10 July 1987	20:15 - 09:30	3	9.6/6.4	13.0 ± 3.0
23 July 1987	22:15 - 08:15	4	10.4/5.8	5.5 ± 3.5

*In addition to these data overnight catches of culicids in four traps operated each night on 14-15 August 1985 and 30 July 1987 were noted as being <10 as collecting containers were emptied and replaced on site. Temperatures at evening start times were 10.0, 9.1 and 9.2, respectively, and overnight lows were 8.6, 6.4 and 3.6 respectively.
#Temperature at evening start time over overnight low.
+These apical container catches represent about 25% of the total culicids trapped.

TABLE 8. Number of culicids and simuliids collected in 5-minute vacuum samples while slowly walking around a CO_2-baited Reindeer model; 10 August 1987*.

Time	No. of culicids	No. of simuliids
19:00-19:05	291	80
19:15-19:20	265	32
19:30-19:35	320	20
19:45-19:50	557	22
20:00-20:05	548	34
20:15-20:20	243	3

*Temperature dropped from 14.2°C at 19:00 to 12.0°C at 20:20.

speeds of 6–8 m/s, 6–10 *C. trompe* males remained active at this mating site throughout the observation period (5 were netted). Some Reindeer exhibited oestrid avoidance behaviors (Table 9), but no female oestrids were seen. The most intense herd reaction to parasitic flies was observed at study area "B" on 27 July 1987, when a herd of about 500 animals was videotaped for 37 minutes between 10:44 and 13:20 h (17°C, 60% cloudy with intermittent sunshine). After foraging periods during which animals exhibited only mild reactions to flies, on five occasions all animals rapidly merged tightly together and broke into a medium to fast trot for 3–5 min. After each bout of trotting, the herd slowed to a walk before starting to disperse and resume foraging.

Zoom lens videotaping of individuals and small groups foraging within 10–50 m of the videotaper helped distinguish reactions to culicids and simuliids from those of oestrids. Within different 5-minute periods, 10 to 30% of the animals exhibited mild culicid/ simuliid responses, but as the animals continued to walk slowly and feed it was apparent that none of these intermittent reactions were serious enough to interfere with foraging. As the herd foraged around and past the videotaper several *H. tarandi* were seen flying and landing on nearby vegetation and one was caught. No *C. trompe* were seen, but there were three instances of animal reactions to *C. trompe*. During the 37 minute videotaped period, the herd spent 27% of the time in fly-associated, non-foraging activities (i.e., trotting or standing in a tightly bunched formation). While dispersed animals were grazing, the videotaped sequence shows nine individuals reacting to *H. tarandi*. Total non-grazing times were not obtained for these animals because of intermittent videotaping of different parts of the herd. In contrast to the mild shakes in response to other flies, animals responded to *H. tarandi* with vigorous body shakes (sometimes with two or three in rapid succession), usually followed by trotting away for several meters and then assuming a stiff-legged, motionless stance for several minutes.

During three 5 min videotaped sequences between 11:00 h and 13:00 h on 28 July 1987 (8°C, and

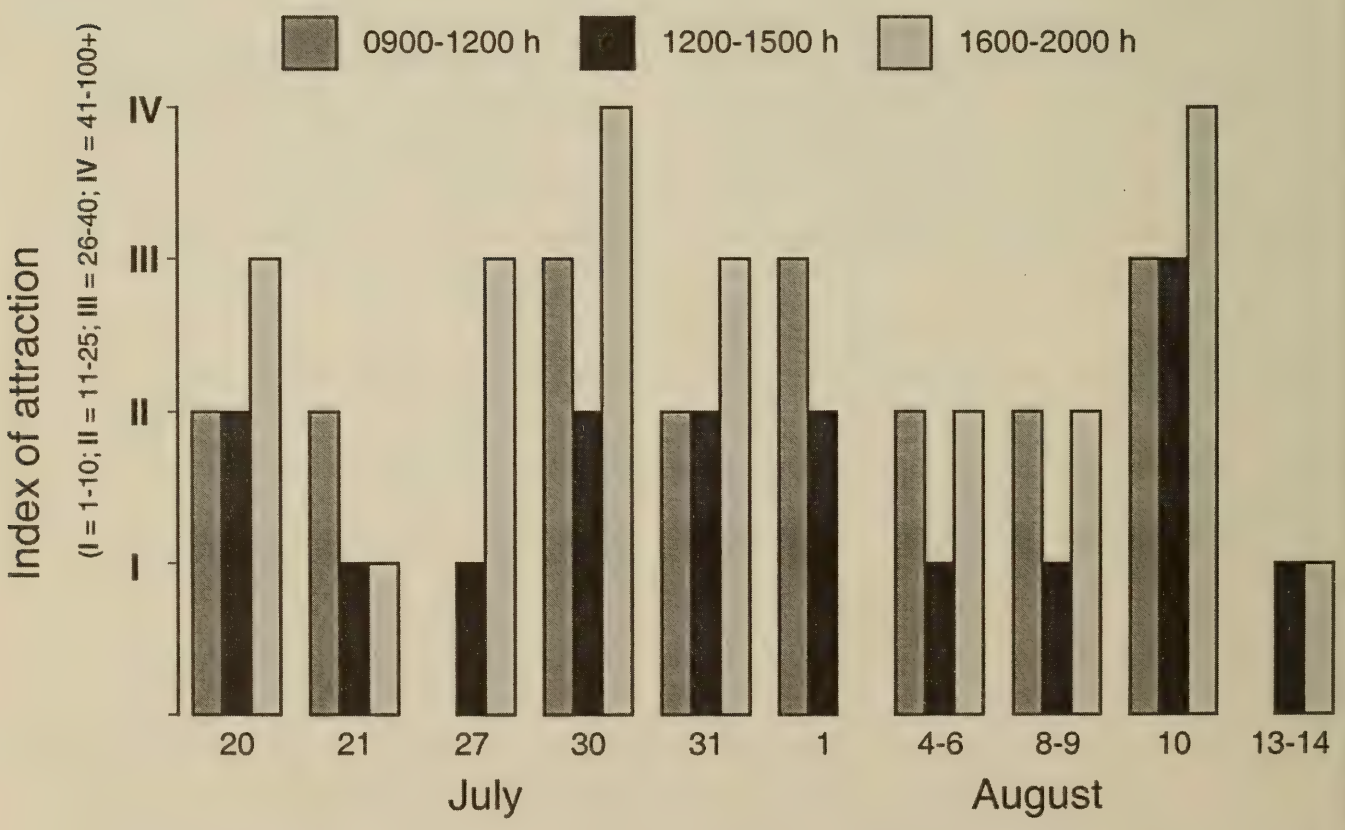

FIGURE 3. Swarming/landing indices of culicids attracted to human in birch/willow woodland (I = 1-10; II = 11-25; III = 26-40; IV = 41-100+). Samples were not taken on cold, rainy days.

TABLE 9. Reactions of Reindeer to inferred attacks by parasitic flies, August 1985.

Date	Time	Observed reactions*
9th	09:20 - 12:15	Five 5 min group scans of 40-50 animals on mountaintop revealed one animal reacting to *C. trompe* and three to *H. tarandi*. Five animals showed reactions to culicids/simuliids.
10th	10:00 - 11:00	None in two 5-minute observations of groups of five and 14 closely dispersed animals.#
11th	18:10 - 18:36	None for three animals observed for 19 minutes, and none for one animal observed for 5 minutes.
13th	11:00 - 12:00	None among 11 closely dispersed animals observed for 21 minutes, 14 observed for 8 minutes and 20 observed for 25 minutes.
	18:00 - 18:15	24% of 8 to 20 closely dispersed animals observed in three 5-minute scans showing 1-2 reactions to culicids/simuliids.
14th	10:00 - 12:00	In ten 5-minute scans of about 100 closely dispersed animals, four reacted to *H. tarandi* and about 25% in each scan showed culicid/simuliid reactions.
	20:15 - 20:50	Five 5-minute observations of two animals showing no reactions.
15th	09:35	None among 19 animals observed for 11 minutes.
	18:00 - 18:25	In two 5-minute scans of 12 closely dispersed animals five exhibited culicid/simuliid reactions.
22nd	10:15 - 10:20	5-minute observation of 42 closely dispersed animals with nine exhibiting culicid/simuliid reactions.
30th	09:30 - 10:00	Two 5-minute observations of five and six closely dispersed animals, with one in each group exhibiting culicid/simuliid reactions.

*_Cephenemyia trompe_ reaction = classic head shaking/lowering response described by Espmark (1961, 1968); _Hypoderma tarandi_ reactions = vigorous body shaking followed by running and then standing motionless in stiff-legged position (some lying and standing animals also jumped); culicid/simuliid reactions = one or more of the following: tail wag/rump shake; leg shake or kick; head shake; ear flicks).

#Animals spaced 2 - 8 m apart.

cloudy bright) no anti-fly behaviors were seen among two groups of 5 and 7 animals lying down, and only 8 of about 100 grazing animals exhibited a reaction to culicids/simuliids. Individual animals videotaped for 5-minute periods while foraging on the vidda between 15:00 h and 17:10 h on 3, 6, and 10 August 1987 (13.4-17.5°C, and mostly sunny) showed only one culicid/simuliid response in two, one and three 5-minute periods, respectively. On 6 August, one animal among a group of five closely spaced animals exhibited a response to *H. tarandi*, and during one of the three 5-minute periods on 10 August, one animal also exhibited a response to *H. tarandi*.

Discussion

Value of CO_2-baited traps as Reindeer mimics

Reports of insect-induced, panicked herd behavior resulting in reduced grazing time of Caribou/Reindeer are common, but unfortunately, circumstances have not permitted concurrent collections of parasitic flies from animals to evaluate which species may be responsible for the observed behavior. In fact, because only a few researchers have collected parasitic flies from tame Reindeer (see Introduction) there are almost no data concerning the guild of parasitic flies associated with Caribou/Reindeer in different geographical areas. For example, although there are at least 26 species of culicids, 38 species of simuliids and 29 species of tabanids known from Alaska, U.S.A. (Sommerman 1958; Gjullin et al. 1961; Burger 1995), with a similar fauna likely in northern Canada (Wood 1985), nothing is known about which, or how many, species of these flies attack Caribou at different times.

In North America, CO_2-baited traps and animal models have attracted and caught the same species of hematophagous flies caught concurrently feeding on Black-Tailed Deer (*Odocoileus hemionus columbianus*) (Anderson and Olkowski 1968; Anderson and Hoy 1972; Anderson et al. 1974), cattle (Roberts 1972; McCreadie et al. 1985; Mason and Kusters 1990) and horses (Anderson and Yee 1995). Moreover, these tools also have proven effective for assessing the seasonal abundance and diel periodicity of species attacking host animals (Anderson and Yee 1995). In Finland, Helle et al. (1992) reported that CO_2-baited traps even caught the same hematophagous species in the same relative abundance as were concurrently caught attacking a tame Reindeer.

In this study CO_2-baited traps caught the same three culicid species caught attacking Reindeer and humans, as well as several tabanid and simuliid species also believed to feed on Reindeer. We previously reported that CO_2-baited traps caught both oestrid parasites of Reindeer (Anderson and Nilssen 1996a) and the same tabanid (*Hy. auripila*) seen attacking Reindeer (Anderson and Nilssen 1998). Other tabanids caught in CO_2-baited traps in this study include three species (*Hy. montana*, *H. pluvialis* and *H. lundbecki*) caught feeding on Reindeer by either Bergman (1915), Breev (1950) or Helle et al. (1992). We therefore conclude that the CO_2-baited traps functioned as effective Reindeer mimics in attracting parasitic flies.

In situations where attacking flies cannot be sampled directly from Caribou/Reindeer, in future studies to assess the impact of different parasitic flies on individual animals and on herd behavior of Caribou/Reindeer, host-mimicking CO_2-baited traps and animal models would be useful in evaluating such factors as the seasonal and proportional abundance, diel activity and the potential negative impact of different flies. Furthermore, because no studies on parasitic flies associated with *R. tarandus* have spanned the entire fly "season", there also is a need for further comparisons of the numbers and species of parasitic flies caught in baited traps (and from animal models) with concurrent collections of flies attacking tame animals in different habitats and in different geographical areas.

Catches of flies at different diel times

In apical collection container catches from 09:30 to 14:30 h versus those from 14:30 to 19:30 h there were significantly more simuliids caught in the second period, but there was no significant difference in the numbers of culicids caught during these periods. Both the diel attack indices for culicids at humans and the few late evening/overnight trap runs completed, established that on warm, sunny days both culicids and simuliids reached peak attacking densities from about 17:00 to 20:00 h, with large numbers of host-seeking culicids remaining active throughout the overnight period. In a related study (Anderson and Nilssen 1998), significantly fewer culicids and simuliids were caught on warm, sunny days from 09:30 to 19:20 h than from 19:20 to 07:00 h the following day, with 94.5% of the culicids and 87.8% of the simuliids caught in the crepuscular/overnight period. By contrast, significantly more tabanids (Anderson and Nilssen 1998) and significantly more *H. tarandi* and *C. trompe* females were caught in first period trap catches than during the second period (Anderson and Nilssen 1996a). This pattern of fly activity is similar to the feeding pattern of tabanids and culicids that attacked cattle in Manitoba, Canada (Ralley et al. 1993).

Comparison of biting fly catches with oestrid catches on different days

Climatic conditions greatly affected the host-seeking activity of different parasitic flies. Warm, sunny/partly sunny days (0 to 75% cloud cover) resulted in large numbers of all parasitic flies being caught in the host-mimicking traps (Tables 3,4) and, by inference, attacking Reindeer. Most oestrids and tabanids were caught on warm (17–25°C), mostly windless and mostly sunny days. These flies were not caught on dark, cloudy days or on days when the temperature was below 10°C. As for oestrids and tabanids, most culicids and simuliids also were caught during warm, sunny days, but primarily during the crepuscular period. However, culicids and simuliids also were caught in large numbers on the many cool, cloudy days when climatic conditions greatly reduced or prohibited the activity of oestrids and tabanids (Tables 3, 4). The culicid/simuliid numbers in Table 3 are smaller than in Table 4 because in 1985 we shut down the traps before the host-seeking activity reached its usual "crepuscular" peak. Anytime the temperature was above 7°C and wind velocities were less than 8 m/s, culicids and simuliids were caught in CO_2-baited traps. From June through August, therefore, there were likely few days when culicids and simuliids did not attack Reindeer. Oestrid attacks, by contrast, were greatly limited by frequent adverse climatic conditions (e.g., darkly overcast, rainy, cold). During our studies such conditions negated oestrid activity on 60% of the days in 1984, 56% of the days in 1985 and 68% of the days in 1987. During a 15-day trapping period near Prudhoe Bay in northern Alaska, Pollard et al. (1996) caught *H. tarandi* on 13 days and *C. trompe* on 8 days at one site, and on only 5 and 3 days, respectively, at another site.

Although stationary traps caught few or no culicids and simuliids on windy days, a mobile tame Reindeer cow was observed being attacked by culicids when vidda wind velocities were 6–10 m/s (with intermittent gusts to 12 m/s). As she walked or trotted from one area to another while foraging, her presence in the new area activated culicids that flew up from the vegetation to attack her, and she intermittently responded with various defensive reactions associated with culicids. When caught and held, no culicids were attracted while the fast wind speeds persisted. This type of opportunistic ambush feeding by culicids in response to the presence of a host that moves into an area where culicids are sheltering permits localized aggregations of culicids to attack Reindeer even on very windy days. The mild anti-culicid behaviors of foraging animals observed on windy day videotape sequences were an indication that they were activating resting culicids as they paused to feed in different areas.

Movements and reactions of reindeer to flies

At study area "A", we observed that, although Reindeer moved from vidda habitat into the woods at times when woods trap catches and the woodland swarming/landing index of culicids at humans were at their peaks, host reactions to flies were not sufficient to interfere with a slow, mobile foraging pace. These observations agree with those of Ardo (1958) who reported that in forested areas of northern Sweden, Reindeer exhibited no apparent avoidance reactions against mosquitoes, but that they tried to avoid tabanids. Because significantly more tabanids were trapped in woodland habitat than on the vidda (Table 2), the daily movement of Reindeer in and out of woodland habitat at study area "A" may have been a response to avoid attacks by large numbers of tabanids. The 1984 mean of 41.5 tabanids/trap/day on the vidda is slightly greater than the 1987 mean of 36.5 tabanids/trap/day, but much less than the 1985 mean of 83.0 tabanids/trap/day (Anderson and Nilssen 1998).

The only times during which we observed panicked, disrupted herd behavior, or observed animals concentrated on mountain tops were between 10:40 and 14:00 h on warm, sunny/partly sunny days. This was when large numbers of both species of oestrid parasites were trapped on such days (Tables 3, 4; Anderson and Nilssen 1996a). If culicids were causing Reindeer to disperse to mountain tops this behavior should have occurred between 16:00 h and 20:00 h, when numbers of host-seeking culicids peaked on warm, sunny days. Although Reindeer on mountain tops may have been trying to avoid oestrids, it was not surprising that they were attacked here because both *H. tarandi* and *C. trompe* are strong fliers (Nilssen and Anderson 1995a). In fact, *C. trompe* mating sites were located on all the high mountain tops in study area "B" (Nilssen and Anderson 1995b), and males were present during periods when Reindeer were observed on mountain tops. Also, 72% of all *H. tarandi* females captured by Downes et al. (1986) were caught on upper slopes and ridgetops. Hughes et al. (1981) reported that horses standing on windy hilltops did not experience a reduction in the number of tabanids harassing them, but further studies are needed to compare the numbers of flies associated with Caribou/Reindeer on mountain tops versus vidda grazing areas.

In Northern Norway female oestrids were the primary cause of the panicked individual and herd behaviors of Reindeer (Anderson and Nilssen 1996a; current study). This conclusion agrees with that of Bergman (1917) in Sweden who noted that neither gnats (i.e., culicids, simuliids and ceratopogonids) nor Tabanidae were the cause of Reindeer becoming so excited on hot summer days and exhibiting the types of reactions and movements he described. He attributed the intense panicked behavioural responses of Reindeer as reactions to the oestrid parasites. More recently, Downes et al., (1986) and Mörschel and Klein (1997) also concluded that oestrids were the primary tormentors of Caribou.

Under the climatic conditions encountered during our studies, and the number of flies caught in traps, we conclude that there were few days when attacks by parasitic flies were intense enough to cause annoyance levels sufficient to reduce overall diel foraging times of Reindeer. As noted by Arnold and Dudzinski (1978) grazing animals usually compensate for reduced daytime grazing time by grazing during night time hours. Although large numbers of hematophagous flies such as simuliids, culicids and tabanids can reduce daytime grazing time of large vertebrates (e.g., Breev 1950; Fredeen 1969; Hughes et al. 1981; Downes et al. 1986; Ralley et al. 1993) the absence or great reductions of such parasitic flies during night time would provide the opportunity for many hours of compensatory grazing. Thus, even on the worst fly days for Reindeer, animals in our study areas had an overnight period of about 6–10 hours during which the small numbers of culicids active then would not interfere with foraging. Because of low temperature, and other climatic conditions unfavorable for flies, during most nights, and on many days, Reindeer in our study area experienced many hours of fly-free foraging time. On the Hardanger vidda in Norway, Thomson (1971) also observed that from 22:30–03:00 h in July (the month when harassment by flies was most serious), Reindeer herds spent 41% of the time grazing and 44% of the time lying

After co-existing with large populations of many parasitic flies for about 2–3 months each year, animals seen in late August/September were in robust, near prime condition (compared to their thin condition in May/June). This indicates that, in our study area, such fly parasites had little or no negative impact on foraging time or weight gain.

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Germination Potential, Updated Population Surveys and Floral, Seed and Seedling Morphology of *Symphyotrichum laurentianum,* the Gulf of St. Lawrence Aster, in the Prince Edward Island National Park

SARAH E. STEWART and CHRISTIAN R. LACROIX[1]

Department of Biology, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island C1A 4P3 Canada
[1]Author to whom correspondence should be addressed.

Stewart, Sarah E., and Christian R. Lacroix. 2001. Germination potential, updated population surveys and floral, seed and seedling morphology of *Symphyotrichum laurentianum,* the Gulf of St. Lawrence Aster, in the Prince Edward Island National Park. Canadian Field-Naturalist 115(2): 287–295.

Symphyotrichum laurentianum, the Gulf of St. Lawrence Aster, is an endemic aster of Prince Edward Island, New Brunswick, and the Magdalene Islands. It is considered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to be of special concern in Canada and to be critically imperiled in Prince Edward Island. One goal of this study was to test germination to clarify the relationship between dormancy and germination in this species. Seeds germinated in culture media had an overall mean percent germination of 68.37% whereas seeds germinated in soil had an overall mean percent germination of 17.38%. Kinetin supplements positively affected germination rates. However, these kinetin supplements eventually led to abnormal morphological development in *S. laurentianum* seedlings. Cold treatments had no significant effects on the percent germination of *S. laurentianum* seeds. Micropropagation of this type of explant and reintroduction should therefore be considered by Prince Edward Island as potential techniques for the conservation of *S. laurentianum* on Prince Edward Island. A complementary goal of this study was to survey the Blooming Point and Covehead sites to update the population statuses of *S. laurentianum* within the Prince Edward Island National Park. The size of the *S. laurentianum* population at Covehead Pond during 1999 was very similar to the population size at this site in 1993. Population sizes showed more fluctuation at Blooming Point between 1993 and 1999. No asters were found in the East Marsh in 1999; however, there was a large increase in population numbers at the Dune Slack site. Seeds of *S. laurentianum* appear to respond well to tissue culture. Annual monitoring of *S. laurentianum* populations should also occur to ensure appropriate management of this species on Prince Edward Island.

Key Words: *Symphyotrichum laurentianum*, Gulf of St. Lawrence Aster, *Aster laurentianus,* seed germination, tissue culture, plant conservation, rare plant, kinetin, micropropagation, Prince Edward Island National Park.

Symphyotrichum laurentianum, Gulf of St. Lawrence Aster, is an annual halophyte endemic to Prince Edward Island, New Brunswick and the Magdalene Islands. Growing in sandy, brackish soils in areas flooded by salt water, *S. laurentianum* is found in salt marshes, around ponds and within dune slacks along the Gulf of St. Lawrence (Fernald 1950; Houle 1988; Houle and Haber 1990; Guignion et al. 1995). The Gulf of St. Lawrence Aster was previously classified as *Aster laurentianus;* however, this species was reclassified by Nesom in 1994. *S. laurentianum* is considered by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) to be of special concern in Canada (Houle and Haber 1990; Guignion et al. 1995; Keith 1998; Shank 1999; Houle and Belleau 2000) and is considered to be critically imperiled within Prince Edward Island (Argus and Pryer 1990).

In 1992 there were six known populations of *S. laurentianum* within the Prince Edward Island National Park (Guignion et al. 1995). These sites included: Covehead Pond, Long Pond, Campbell's Pond, Blooming Point Western Wetland, Blooming Point East Marsh and Blooming Point Dune Slack. Population estimates for *S. laurentianum* at the Blooming Point Eastern Marsh in both 1992 and 1993 were 48 000- 60 000, while the Blooming Point Dune Slack site had an estimated population size of 15 000- 20 000. The four other populations of *S. laurentianum* within the Prince Edward Island National Park had much smaller population sizes than the populations occurring at Blooming Point. In 1993, there were 214 *S. laurentianum* plants in the Covehead Pond population, while only one plant was found at Long Pond. Three *S. laurentianum* plants were found at Campbell's Pond in 1993 while no plants were found at the Blooming Point Western Wetland, a site once reported to have Gulf of St. Lawrence Asters. Population sizes within some sites also greatly fluctuated between years (Guignion et al. 1995).

One of the main factors affecting population size in vascular plants species, especially annuals, is the germination potential of the seeds they produce. Houle and Haber (1990) reported an 80% germination for *S. laurentianum* seeds. A percent germination of over 50 has also been reported for this species by Houle and Belleau (2000). It is well known that

before germination is triggered, seeds of many vascular plant species require a dormancy period. *S. laurentianum* seeds mature in October and do not germinate until the middle of the following June. This indicates that *S. laurentianum* seeds have some mechanism which either prevents germination or does not induce germination until that time. Cold treatments and treatments with growth hormones, such as gibberellic acid and kinetin, have been used to overcome dormancy periods in other vascular plant species (Baskin and Baskin 1998).

The objectives of this study are: (1) to perform germination tests to clarify the relationship between dormancy and germination in *S. laurentianum* seeds by using cold treatments, and treatments with kinetin and gibberellic acid to trigger the highest germination rates possible for this species and (2) to survey the Blooming Point and Covehead sites to update the population statuses of *S. laurentianum* within the Prince Edward Island National Park.

Materials and Methods

Population Studies

Due to the low reported population numbers of *S. laurentianum* at Covehead Pond (46° 25' 47" N; 63° 9' 11" W) a total population count was conducted at this site. The height of each plant was measured as well as the distance of each plant from the pond water's edge. A total count of the number of inflorescences per plant was also recorded.

At Blooming Point, the Western Wetland (46°24' 56" N; 62°58'44"W; 46°24'56"N, 62°59'6"W), Dune Slack (46°24'52"N; 62°59'42"W) and Eastern Marsh sites coordinates were all surveyed for *S. laurentianum* plants. Due to the large numbers of individuals in these populations, total population counts were not feasible. Instead, population estimates were carried out at these locations. Five 0.5 m^2 plots were randomly chosen in the Dune Slack site and in the Eastern Marsh. Population sizes were estimated using marsh areas calculated by a global positioning system (GPS) and the average number of plants found in the 0.5 m^2 plots. Longitudinal and latitudinal coordinates were also recorded using a GPS.

Seed Collection and Treatment

Symphyotrichum laurentianum seeds were randomly collected from Covehead Pond, Blooming Point Dune Slack and Blooming Point East Marsh sites in the Prince Edward Island National Park. Half of the seeds were randomly chosen to represent the control group which was kept at room temperature until germination tests were performed. The remaining half of the seeds were placed in a refrigerator maintained at 4° C until germination tests were performed. This time period ranged from one month to eight months depending on replication number.

Seeds in Soil

Fifty seeds from each of the two treatment groups were randomly selected and were planted in labelled pots filled with equal parts vermiculite, peat moss and potting soil. A further 50 seeds from each of the two treatment groups were randomly selected and underwent a treatment in 30 ml of a 5mg/100ml gibberellic acid solution for 25 hours. Pots were placed in a Conviron Model E 15 growth chamber set at 25°C, 80% humidity and on a light/ dark schedule of 16/8 hours. Four trials of this procedure were repeated. A modified version of this protocol was carried out two additional times to duplicate Houle and Belleau's (2000) germination study. In this situation the pots were placed in a growth chamber set at 80% humidity, on a light/dark schedule of 14/10 hours and at light/dark temperatures of 19/13° C. Germination was considered successful when seedlings emerged from the soil.

Seeds Germinated in Petri Dish

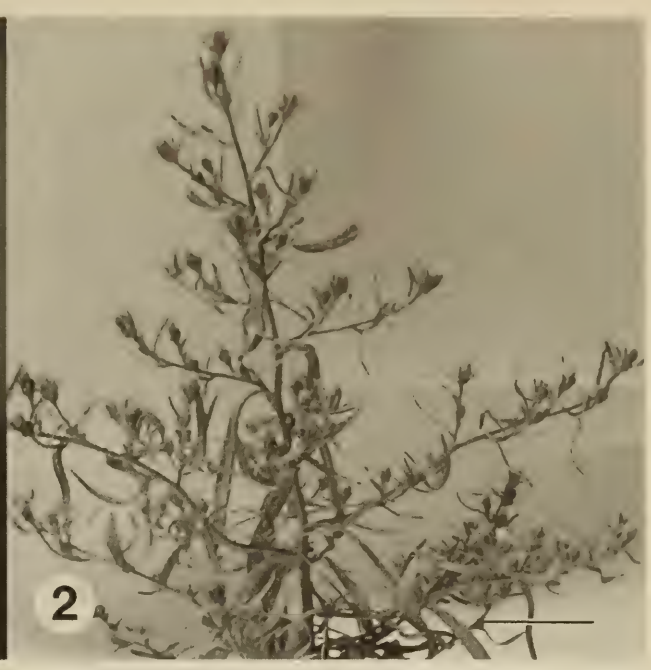
Fifty seeds were randomly chosen from the room temperature group and the cold treatment group. Seeds were placed in separate labelled petri plates, on two layers of filter paper and covered with distilled water. Plates were placed in a growth chamber set at 80% humidity, on a light/dark schedule of 14/10 hours and at light/dark temperatures of 19/13° C. This procedure was repeated twice for a total of three trials. Successful germination was considered when the radicle emerged from the seed coat.

Seeds in Growth Media

Seeds from both treatment groups were randomly selected and were cultured on Murashige and Skoog Basal Salt Media (1962), at quarter strength, half strength and full strength concentrations, supplemented with either no kinetin, 2 mg/l kinetin, or 4 mg/l kinetin. All media were also supplemented with standard basic additives: 0.02 g thiamine, 0.04 g myo- inositol, 30.0 g sucrose and 10 g gelrite. The growth medium was autoclaved for 30 minutes at 121° C and was poured into petri plates and sealed with Parafilm M to prevent contamination and dehydration. Prior to culturing, seeds were sterilized in a 5.25% sodium hypochlorite solution and Triton-X-100 nonionic surfactant for 35 minutes. The seeds were then soaked in one wash of sterile distilled water for three minutes. Plates containing seeds were placed in a growth chamber at 25° C, 80% humidity and on a light/dark schedule of 16/8 hours. Germination was considered successful when the radicle emerged from the seed.

Morphological Analysis

Seeds of *S. laurentianum* at various stages of dissection were dehydrated in a graded ethanol series and critical point dried using CO_2 as a transitional fluid in a model 28000 LADD critical point dryer. Specimens were mounted on stubs, grounded with silver paint, then coated with 300 Angstroms of gold-palladium using a Denton Vacuum Desk II sputter-



FIGURES 1-2. Macroscopic view of *Symphyotrichum laurentianum* plant and inflorescence. (1) White capitulum (arrowhead) of *Symphyotrichum laurentianum*. (2) Multibranching specimen of *Symphyotrichum laurentianum*. Scale bars represent 5 mm (1) and 75 mm (2).

coater. Specimens were examined with a Cambridge Stereoscan 604 scanning electron microscope, and thermal prints of the digital SEM images were acquired using SEMICAPS© software and produced using a Mitsubishi P67U video copy processor.

An Olympus SZ40 microscope equipped with a Pixera Digital Camera system was used to photograph *S. laurentianum* plants grown in culture from germination to early stages of shoot growth.

Statistical Analysis

T-tests with Bonferonni correction were performed to compare mean percent germination between seeds in different treatment groups.

Results

Population Information

A total of 243 *S. laurentianum* plants (Figure 2) were found at the Covehead Pond site in 1999. The height of *S. laurentianum* plants at this site ranged from 2.5 cm to 46.0 cm. The mean height of *S. laurentianum* plants at the site was 12.7 cm ± 6.85 (n=243). The number of inflorescences per plant at the Covehead site ranged from 0 to 729 while the mean number of inflorescences per plant was 15.42. *S. laurentianum* plants at Covehead Pond were found anywhere from 5 cm to 1010 cm from the edge of the pond. The mean distance between the pond's waterline and *S. laurentianum* plants at Covehead was 644.02 cm ± 311.16 (n=243). All of the aster inflorescences at both the Covehead site and the Blooming Point sites were white (Figure 1). Refer to Table 1 for Blooming Point population size comparisons.

Seed Germination in Soil

S. laurentianum seeds planted in soil in the growth chamber had an overall mean percent germination of 17.38% ± 9.51 (n=800). There were no significant differences between the mean percent germination of seeds in the control group and the mean percent germination of seeds in any of the other three treatment groups (t-test; $p > 0.05$). Seeds treated with a cold treatment prior to planting had a significantly higher mean percent germination than seeds that underwent both the cold treatment and the treatment with gibberellic acid (t-test; $p < 0.05$). Seeds that were left at room temperature and then were treated with gib-

TABLE 1. Comparison of population sizes for *Symphyotrichum laurentianum* in Prince Edward Island.

Population	1992	1993	1999
Covehead Pond	168	214	243
Western Wetland	425	0	0
Dune Slack	15- 20 000*	15- 20 000*	65 250*
East Marsh	50- 60 000*	50- 60 000*	25 000*

*estimated.

TABLE 2. Mean percent germination of *Symphyotrichum laurentianum* seeds planted in soil.

Treatment	Mean Percent Germination
Control[a]	16.5 ± 9.98
Cold Treatment[b,d]	22.5 ± 7.19
Control + GA_3 Treatment[b,d]	20.0 ± 12.44
Cold + GA_3 Treatment[d]	10.5 ± 6.19

Note: Treatments with the same letter superscripts are significantly different from one another.

berellic acid also had a significantly higher mean percent germination than seeds that were treated with both a cold treatment and a treatment with gibberellic acid (t-test; $p< 0.05$)(Table 2).

Seeds maintained in the growth chamber as specified by Houle and Belleau (2000) had an overall mean percent germination of 36.0% ±16.14 (n= 400).

Seed germination in petri plates

Seeds germinated in petri plates had an overall mean percent germination of 15.33% ± 9.35% (n=300). There was no significant difference between the mean percent germination of seeds kept at room temperature and the mean percent germination of seeds subjected to a cold treatment (t-test; $p> 0.05$).

Seed germination in culture

The overall mean percent germination of all seeds in culture was 68.37% ± 26.38% (n=821). The mean percent germination of seeds maintained at room temperature prior to culturing was 84.88% ± 16.31% (n=369). The mean percent germination of seeds treated with a cold treatment prior to culturing was 51.85% ± 24.21% (n=452). The difference between these two mean percent germinations was not statistically significant (t-test; $p>0.05$).

Seeds grown in quarter strength basal salt media in both the room temperature and cold treatment groups had significantly higher mean percent germinations than seeds grown in full strength media (t-test; $p<0.05$). In the room temperature group, seeds grown in quarter strength media also had significantly higher mean percent germination than seeds grown in half strength media (t-test; $p<0.05$).

Within the room temperature group in both full strength and half strength media, seeds grown in media supplemented with 2 mg/l kinetin had significantly higher mean percent germination than seeds grown in media that was not supplemented with kinetin (t-test; $p<0.05$). Seeds grown in full strength media supplemented with 4 mg/l kinetin also had significantly higher mean percent germination than seeds grown in full strength media which did not contain a kinetin supplement (t-test; $p<0.05$).

There were no statistically significant differences between the mean percent germination of any of the seeds grown in different media strengths or different kinetin strengths within the cold treatment group (t-test; $p>0.05$). See Table 3 for a summary of the tissue culture results.

Morphology

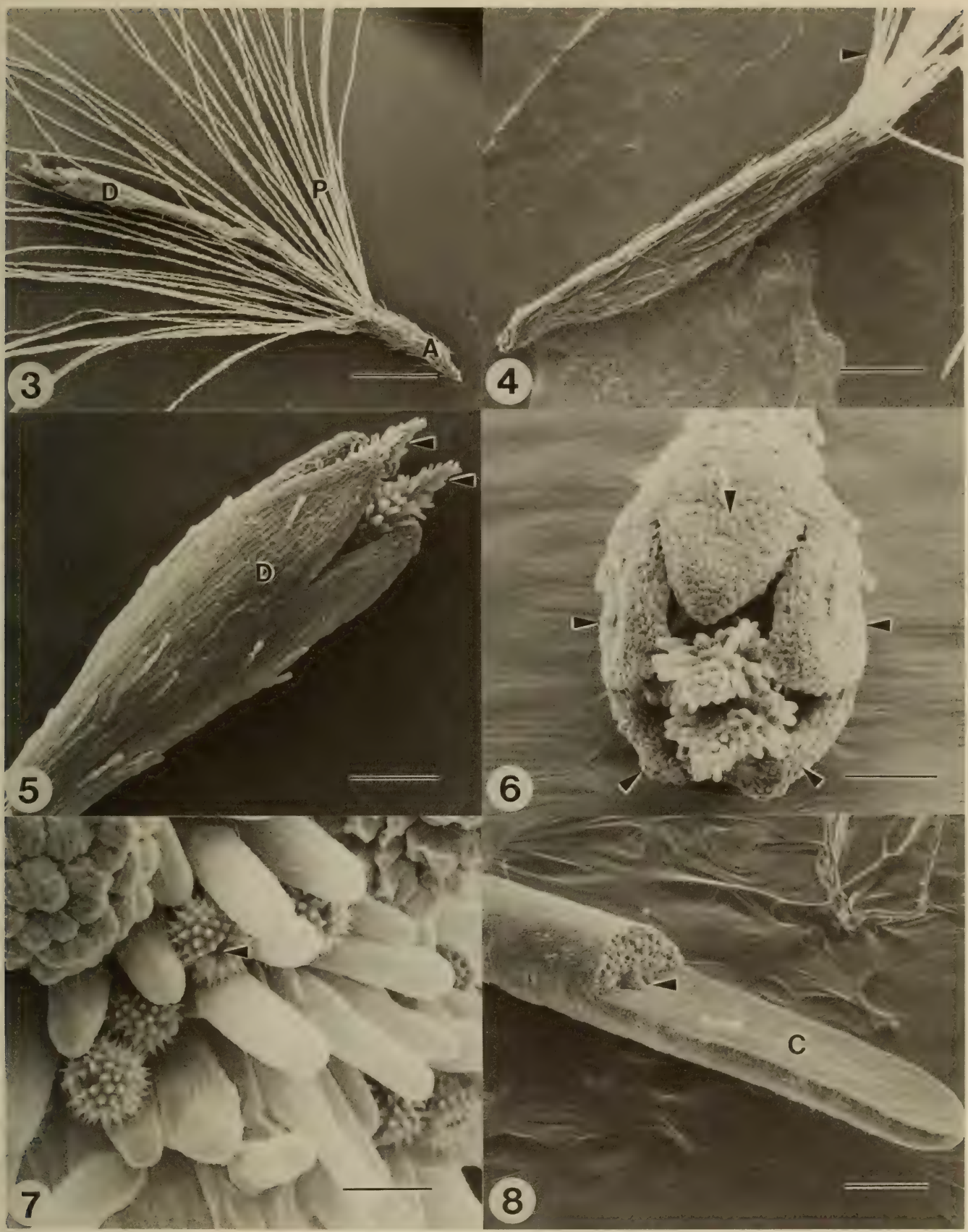
Seeds: Symphyotrichum laurentianum achenes (Figure 4) have a mean length of 2.09 mm ± 0.15 (n =30). Mature embryos are surrounded by a clear seed coat, and the seeds are encased in a hard fruit wall. The achenes are attached to a pappus composed of white barbed bristles (Figure 3) which have a mean length of 4.93 mm ± 0.57 (n=30). Two long, flat and closely appressed cotyledons cover the shoot tip of the seed embryo which is oriented towards the pappus. A shoot meristem is visible between the two cotyledons in the mature seed but no leaf primordia are visible (Figure 8).

Florets: All inflorescences consist entirely of disc florets (Figure 5). Each disc floret is surrounded by a pappus which is longer than the floret. Mean floret length is 3.74 mm ± 0.22 (n=30). The corolla of tube florets is five lobed and shorter than the style (Figure 6). Two stigmas containing pollen collecting papillae extend above the corolla of each tube floret. Anthers

TABLE 3. Mean percent germination of *Symphyotrichum laurentianum* seeds in culture.

Treatment Group	Mean	Media Strength	Mean	Kinetin Supplement	Mean
Control[a]	84.9 ± 16.3	Full MS[c]	74.6 ± 22.3	no kinetin[g,h]	50.7 ± 18.8
				2 mg/l kinetin[g]	83.1 ± 15.0
				4 mg/l kinetin[h]	90.0 ± 10.0
		1/2 MS[d]	85.6 ± 10.2	no kinetin[i]	77.5 ± 9.7
				2 mg/l kinetin[i]	93.3 ± 11.5
				4 mg/l kinetin[j]	86.0 ± 175
		1/4 MS[c,d]	94.4 ± 6.2	no kinetin[k]	95.2 ± 8.3
				2 mg/l kinetin[l]	96.4 ± 3.2
				4 mg/l kinetin[m]	91.6 ± 7.6
Cold[b]	51.8 ± 24.2	Full MS[e]	39.8 ± 25.5	no kinetin[n]	38.0 ± 15.3
				2 mg/l kinetin[o]	31.6 ± 13.3
				4 mg/l kinetin[p]	49.7 ± 44.1
		1/2 MS[f]	51.4 ± 27.6	no kinetin[q]	55.2 ± 13.0
				2 mg/l kinetin[r]	41.3 ± 44.4
				4 mg/l kinetin[s]	57.7 ± 25.8
		1/4 MS[e]	64.4 ± 12.3	no kinetin[t]	58.8 ± 7.0
				2 mg/l kinetin[u]	70.1 ± 8.7
				4 mg/l kinetin[v]	64.3 ± 19.7

Note: Treatments with the same letter superscripts are significantly different from one another.



FIGURES 3-8. Floret and fruit of *Symphyotrichum laurentianum*. (3) *Symphyotrichum laurentianum* fruit showing achene (A), pappus (P) and wilted remains of disc floret (D). (4) Achene showing pubescent fruit coat and barbed pappus (arrowhead). (5) Stigmas (arrowheads) protruding from the disc floret (D). (6) Five continuous petals (arrowheads) make up the corolla of the disc floret. (7) Pollen with apertures (arrowhead) caught in the papillae of the stigma. (8) Embryo with one cotyledon removed revealing the apical meristem (arrowhead). C= cotyledon. Scale bars represent 750 μm (3), 300 μm (4), 75 μm (5), 75 μm (6), 15 μm (7), 150 μm (8).

are connate and introrse and surround the stigmas inside of the corolla tube.

Pollen: Symphyotrichum laurentianum pollen grains are circular, with trizonoporate apertures and echinae sculpturing, which is typical of many members of the Asteraceae (Figure 7).

Seedling: The reddish-brown fruit walls of *Symphyotrichum laurentianum* seeds become clear as seeds imbibe water. Cotyledons become greener and can be seen through the translucent fruit wall (Figure 9). These features can be observed less than 24 hours after seeds are placed in media. Following these initial stages, the hypocotyl of the embryo axis extends through the achene and cotyledons begin to separate causing the fruit wall to split and be shed (Figure 10). This stage takes place less than 48 hours after seeds are introduced in the media.

During the following 24 to 72 hours, cotyledons separate further and the hypocotyl continues to elongate. After four to six days in media, root elongation takes place followed by the formation of many root hairs (Figure 12). As early as five days in media or as late as ten days, the first true foliage leaves are visible in some seedlings. The second true foliage leaf was not observed until after seedlings had been in media for at least 12 days (Figure 14).

Seedling Abnormalities: Root elongation was suppressed in all seedlings grown in media which contained a kinetin supplement. However, root hairs did form on the radicle of these seedlings (Figure 11). Stem elongation was also suppressed in all seedlings grown in kinetin supplemented media (Figure 13).

Discussion

Population Information

Populations of *S. laurentianum* within the Prince Edward Island National Park have fluctuated and changed significantly over the last eight to ten years.

Covehead: The *S. laurentianum* population at Covehead Pond has been slightly increasing over the past ten years. This site consisted of 168 *Symphyotrichum laurentianum* plants in 1992, 214 plants in 1993 (Jacques Whitford 1994), and 243 plants in 1999. The *Symphyotrichum laurentianum* population at Covehead occupies an area of approximately 320 m^2. The average density of *Symphyotrichum laurentianum* plants along the north and east sides of the pond is approximately 0.759 plants per m^2. All of these *S. laurentianum* plants grow in an area frequently flooded by salt water.

Although this *S. laurentianum* population is increasing, it is still well below the population size of 500 recommended by Given (1994) as stable and self sustaining for vascular plants species. Annual monitoring of this site is recommended to ensure that the Covehead population of *S. laurentianum* is not lost.

Blooming Point: The population of *S. laurentianum* at the Blooming Point Western Wetland was lost in 1993 due to drier conditions in this marsh (Jacques Whitford 1994). Further evidence that the marshes in the Blooming Point area are becoming drier is the disappearance of a stream which ran through the East Marsh in 1992 and 1993. A decrease in habitat size at the East Marsh has also occurred over the past few years. The original six pockets of *S. laurentianum* at this site in 1993 were reduced to two pockets in 1999. Drought stress has been shown to be a limiting factor for this species (Houle and Belleau 2000). Drier conditions in this marsh may be contributing to the decline of suitable habitats for *S. laurentianum* at Blooming Point.

The estimated population size of 65 250 asters at the Blooming Point Dune Slack site in 1999 is much larger than the estimated population size of 15 000 - 20 000 plants at this site in 1993. The *S. laurentianum* population at this site is extremely dense with an average of 160 plants per square meter. This is a much higher density than that of the Covehead population. However the aster plants at Blooming Point were much smaller and had fewer branches than the plants at Covehead.

The *S. laurentianum* populations at Blooming Point are located along a peninsula which is relatively secluded from public areas. Disturbance by humans is not believed to be a factor that may contribute to the decline of populations at this location. However, human activities in and surrounding Tracadie Harbour may have the potential to directly affect the populations of *S. laurentianum* along the Blooming Point peninsula especially if future developments in the Tracadie Harbour area are considered. Blooming Point is an extremely important site for *S. laurentianum* on Prince Edward Island. It is critical for the perpetuation of this species on Prince Edward Island that these populations remain viable. The Blooming Point peninsula must continue to be monitored and protected to ensure that these marshes remain suitable habitats for this vulnerable species.

Based on the population information available to date, it is recommended that *Symphyotrichum laurentianum* remain classified as critically imperiled on Prince Edward Island. Only three populations of *Symphyotrichum laurentianum* have been documented on P.E.I. in recent years which clearly places the Gulf of St. Lawrence Aster within this risk category.

Seed germination

The overall germination test results from soil and culture media trials reported in this study are lower than those reported in other studies. For example, Houle (1988) reported an 80% mean percent germination in *S. laurentianum* seeds and Houle and Belleau (2000) were able to achieve a mean percent germination of over 50%. Houle (1988) does not include the parameters surrounding the seed germination compo-

FIGURES 9-14. Developmental sequence of *Symphyotrichum laurentianum* seedlings grown in MS culture media. (9) Seed germinating in culture medium. Note the seed (arrowhead) inside the transparent, pubescent fruit coat (arrowhead). (10) Seedling after six days in culture showing the cotyledons beginning to separate. R= radicle. (11) Seedling after five days in culture medium containing a kinetin supplement. Root hairs are present on the radicle (R) but root elongation is inhibited. (12) Seedling after six days in culture media which did not contain a kinetin supplement. Root elongation is not inhibited (arrowheads). (13) Seedling after 74 days in culture medium containing a kinetin supplement. Stem elongation is inhibited and leaves are consequently crowded. (14) Seedling after 51 days in media which did not contain a kinetin supplement. Stem elongation is not inhibited in this seedling. Scale bars represent 0.5 mm (9), 0.7 mm (10, 11), 0.9 mm (12), and 10 mm (13, 14).

nent of her study making it difficult to duplicate her seed germination experiments. While all of the seeds in our study were collected from Prince Edward Island, seeds in Houle's (1988) study and Houle and Belleau's (2000) study were collected from the Magdalene Islands. It is possible that these two populations have different reproductive capacities.

Seeds grown in tissue culture had a significantly higher mean percent germination than seeds grown in soil. In tissue culture conditions seeds are completely surrounded by growth media which provides a higher surface area for osmosis and a balanced abundance of essential minerals and nutrients. The higher mean percent germination of seeds in quarter and half strength MS media as opposed to mean percent germination of seeds in full strength MS media may also be linked to the role of osmosis in seed germination. Half strength and quarter strength media have a lower solute/solvent ratio than full strength media. A low solute/solvent ratio in the media leads to a lower water potential in the seed than in the surrounding media, causing water to flow into the seed and allowing the process of imbibition to take place. For future micropropagation projects involving *S. laurentianum* it is recommended that half or quarter strength MS media be used.

Seeds grown in MS media supplemented with kinetin had higher percent germination than seeds grown in media without kinetin. Kinetin has been used as an agent to break dormancy in seeds of many plant species (Phillips 1971; Webb et al. 1973; Bewley and Black 1985). Supplements of 2 mg/l and 4 mg/l of kinetin were used in this study to induce shoot formation. It was believed that the high concentrations of the exogenous kinetin supplements in combination with the generally low endogenous levels of auxin present in the seed would induce the initiation of shoot meristems. However, both shoot and root elongation were inhibited in *A. laurentianus* seedlings growing in media containing kinetin supplements. High levels of plant growth hormones have been known to inhibit growth altogether in other species (Yeoman 1973). While kinetin levels of 2 mg/l and 4 mg/l were sufficient to induce shoot elongation in other species (Amo-Marco and Ibañez 1998), it is possible that these levels are too high for *Symphyotrichum laurentianum*. Supplements of plant growth hormones have also produced abnormal morphological development in other plant species (Amo-Marco and Ibañez 1998). Due to kinetin's positive effect in increasing mean percent germination in *S. laurentianum* it is recommended that kinetin be initially present in media to increase germination rates in this species. However, immediately following germination, seeds should be transferred to a kinetin free medium to ensure that root and shoot elongation are uninhibited.

Symphyotrichum laurentianum seeds do not appear to benefit from cold treatments or treatments with gibberellic acid. In natural conditions *S. laurentianum* seeds do not germinate until late June, so perhaps it is the warming conditions in the spring which induce germination in this species. We would therefore recommend that future studies include a heat treatment in any germination tests involving the Gulf of St. Lawrence Aster.

Tissue culture is a simple, inexpensive and potentially useful tool to mass propagate *S. laurentianum* from seed. Although other vegetative tissue sources may also be explored, seeds are the recommended source for germination programs as they carry the maximum genetic diversity to offspring (Fay 1991). Plants grown using micropropagation techniques could be reintroduced into wild populations in an attempt to stabilize vulnerable populations. Micropropagation and reintroduction programs have been used in past projects involving plant conservation (Nandi et al. 1999; Nadeem et al. 2000). Micropropagation of *Senecio hadrosomus, Atractylis arbuscula* var. *shizogynophylla, Artemisia granatensis* and *Psiada coronopus*, all rare members of the Asteraceae, has been successful in several conservation projects (Fay 1991). Based on these conservation projects and our preliminary tissue culture data, there is potential that *Symphyotrichum laurentianum* may also be successfully conserved through a micropropagation and reintroduction program.

Acknowledgments

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Mule, *Odocoileus hemionus*, and White-tailed, *O. virginianus*, Deer in the Yukon

MANFRED HOEFS

Yukon Fish and Wildlife Branch, Box 2703, Whitehorse, Yukon Y1A 2C6 Canada

Hoefs, Manfred. 2001. Mule, *Odocoileus hemionus*, and White-tailed, *O. virginianus*, deer in the Yukon. Canadian Field-Naturalist 115(2): 296–300.

Both Mule Deer (*Odocoileus hemionus*) and White-tailed Deer (*Odocoileus virginianus*) have colonized the southern half of the Yukon in recent decades. Mule Deer have attained a continuous distribution in suitable habitats, White-tailed Deer have remained rare. Deer habitats are largely open, south-facing grassy slopes bordered by aspen, sites of recent forest fires, and cultivated hay fields. Many sightings have been reported by the general public. These have been supplemented by interviews of native elders and other long-time residents and a literature search. Mule Deer first appeared in the Yukon in the late 1930s to early 1940s and by the 1980s had reached the latitude of Dawson (64° N) and crossed into Alaska in the Ladue River drainage. A northern record for Mule Deer was established with a sighting near Chapman Lake along the Dempster Highway (64° 50' N, 138° 25" W). White-tailed Deer are more recent, first observed near the British Columbia border (60° 10' N) at Tagish Lake in 1975 and reaching Moose Creek along the Klondike Highway (63° 30' N) in 1998.

Key Words: Mule Deer, *Odocoileus hemionus*, White-tailed Deer, *Odocoileus virginianus*, Yukon, range extension, traffic mortalities.

Deer are a new addition to Yukon's large mammal fauna. They have invaded and colonized much of the southern half of this Territory over the past 50 to 60 years. Both Mule Deer (*Odocoileus hemionus*) and White-tailed Deer (*Odocoileus virginianus)* are present, but Mule Deer are more common. Little attention has been paid to their presence within the Yukon nor outside. Recent scientific publications about deer (Whitaker 1980; Hesselton and Hesselton 1982; Mackie et al. 1982) do not include the Yukon as part of their range, and management efforts by government have been "low key". The Yukon Territory has a small population and limited resources and has had to focus its efforts on economically important species, while deer are relatively rare and protected from hunting. The information collected about deer, therefore, consists largely of voluntary contributions, either by government staff collecting data concurrently with other field studies, or by members of the general public reporting deer sightings.

Methods

Information about deer in the Yukon was collected by: (1) ongoing cataloguing and mapping of deer sightings, (2) collecting records of road mortalities, (3) questionnaires and interviews, and (4) literature search. In the 1960s the newly established wildlife management agency began to record deer sightings made by its staff or reported by the general public. Independently, Conservation Officers, RCMP Officers, and highway maintenance staff recorded deer mortalities resulting from collisions with vehicles along Yukon's major highways. Incidental sightings as a data source was improved over the years by incorporating questionnaires and public education, and by recording interviews with native elders and other long-term residents. Reports by biologists, geologists, and fur traders, as well as books published by big game hunters going back to the turn of the century were searched for references to deer. To verify the presence of White-tailed Deer in addition to the more common Mule Deer, tissue samples of the former were submitted to the Forensic Laboratory, Alberta Natural Resources Service, Edmonton, for species identification by DNA analyses.

Results

Over the past 40 years, 391 records were filed by the Yukon Fish and Wildlife Branch reflecting 1101 deer sightings. About 80% of these were observations of Mule Deer (Figure 1), 19 were documentations of White-tailed Deer (Figure 2), and the remainder were non-specific. Most observations (N = 737) did not attempt a break-down into sex and age classes; those that did (N = 373) revealed the following population structure: 105 bucks, 190 does, and 69 fawns. Single deer were most frequently observed (N = 136), followed by pairs (N=51). A negative linear correlation followed (R = -0.722) between increasing group size and decreasing frequency of observation, ranging from 35 observations of groups with three deer to two observation of groups with over 20 deer. The numbers of observations reported fluctuated greatly between years. However, if they are lumped by five-year intervals or by decades a steady increase was evident: from only one observation prior to 1960 to over 500 during the most recent decade (Figure 3).

FIGURE 1. Mule Deer buck along the Takhini Hotspring Road west of Whitehorse. This is a high-density deer area, presumably because of the local agricultural activity.

The number of deer killed in collisions with vehicles showed a parallel trend. Only two mortalities were recorded prior to 1975, while 54 deer were killed over the past five years (1995–1999) (Figure 4). Deer were observed during every month, but most often during September. This was also the month when most were killed in accidents (Table 1). Interviews with old-timers corroborate this documentation. The late Johnny Johns (Carcross), native elder and big game guide, remembered seeing his first deer near Judas Creek in the early 1940s. A. VanBibber (Champagne) reported several sightings in the Takhini River area west of Whitehorse in the late 1940s and early 1950s. Clyde Blackjack (Carmacks) saw his first deer along the Yukon River between Lake Laberge and Big Salmon in summer 1945. The late Phil Temple (Kluane) remembered observing a deer at the Junction of the Little River with the Takhini River in 1953. Dan Nowlan (Watson Lake) reported a deer during a hunting trip 60 miles up the Liard River

FIGURE 2. Skull of a male White-tailed Deer found north of Ross River by Ron Etzel in February 1997.

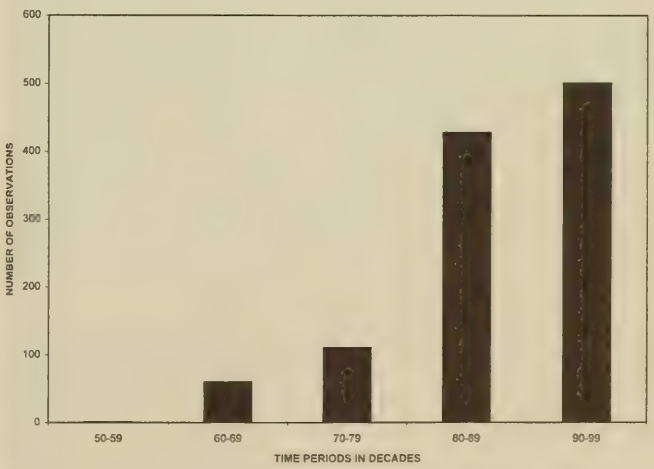

FIGURE 3. Number of deer sightings reported to the Yukon Wildlife Branch since record keeping began in the 1950s.

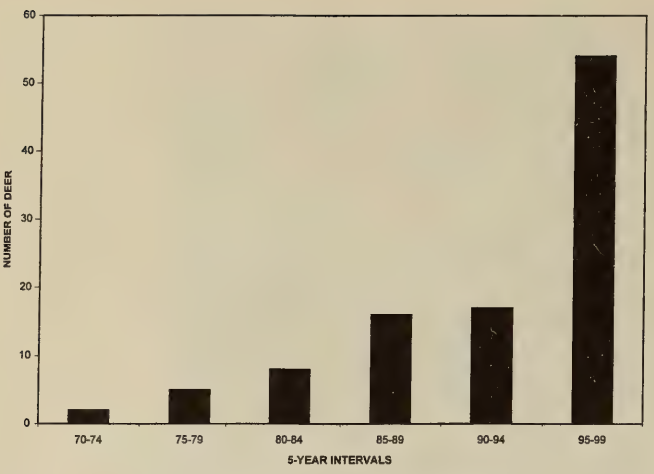

FIGURE 4. Number of deer killed in collisions with vehicles along Yukon's major highways since record keeping began in the early 1970s.

in the early 1950s. Nowlan was accompanied by the late George Dalziel on this trip, who apparently saw three deer on this occasion.

The first published reference to deer is found in Rand (1944), who reported second-hand information from the following localities along the newly constructed South Alaska Highway: Bucking Horse River, Steamboat Mountain, Summit Pass, Lower Liard Crossing, and Coal River. The latter two locations were close to the Yukon border. Clarke (1946*) assumed that deer had crossed into the Yukon in these areas. Clarke (1946*) also reported deer within the Yukon from the Nisutlin River and the Teslin area. Youngman (1975) summarized anecdotal information about deer to the early 1970s and listed records from Ross River, Carmacks and the Takhini River west of Whitehorse.

Discussion

Mule Deer have colonized most suitable habitats in the southern Yukon, with the latitude of Dawson (64°) constituting the northern limit of their current distribution (Figure 5). The notable exception is the record of a Mule Deer doe and her fawn along the Dempster Highway near Chapman Lake (64° 50'N, 138° 25"W) by M. Villeneuve in summer 1998. This is the northernmost record for this species. To the west, Mule Deer have crossed the border into Alaska, most likely following the valley of the Ladue River upstream toward Tok during the 1980s. It is assumed that they first entered the Yukon from the Liard River drainage of northern British Columbia in the late 1930s to early 1940s.

White-tailed Deer were first observed in 1975 by W. Ward at Tagish Lake, only a few miles north of the British Columbia border. The northern-most sighting, made in 1998, comes from Moose Creek near Stewart Crossing. Using straight-line distances their rate of colonization averaged 25 km/year, exceeding that of Mule Deer with 17 km/year.

Most deer were observed in open areas such as south-facing grassy slopes with thin snow cover, sites with early successional vegetation such as recently burnt forests, agricultural fields seeded with forage crops, and re-vegetated road allowances. Numbers of deer observed (Figure 3) and numbers of deer lost in traffic accidents (Figure 4) have increased since record taking began in the 1960s and 1970s. However, this upward trend only in part reflects a growing population and an expanding distribution; it also shows increasing interest by the public and a greater willingness to report sightings, as well as greater effort by government to collect this information.

While the distribution map of deer (Figure 5) is fairly reliable, it overestimates the area actually inhabited by them, since it is based on game management zones in which deer have been reported and not on point locations. A reliable estimation of numbers was not possible with the information at hand, and it appears that these also fluctuate greatly between years, apparently reflecting winter severity. An educated guess places their number at 500 to 800, of which fewer than 100 may be White-tailed Deer (Hoefs 2000*).

The population structure of 105 ♂: 190 ♀: 69 fawns is within the reported range, but it is somewhat distorted. For an non-hunted population, the number of bucks is low compared to number of does. Also the ratio of fawns to does is low, considering that twinning is frequent in deer. However, not too much reliability can be placed on these numbers, which are averages from 30 years of records and may not reflect current population dynamics.

The annual periodicity of deer observations and traffic mortalities, which are significantly correlated (R = 0.792), are assumed to reflect deer activity as well as demographics (Table 1). In late winter observations were few and traffic losses low. Deer move-

Table 1. Annual peridicity of deer observations and traffic mortalities.

		Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	**Total**
Deer Observed	N	17	12	11	22	19	20	34	17	64	26	18	18	278
	%	6.1	4.3	4.0	7.9	6.8	7.2	12.2	6.1	23.0	9.4	6.5	6.5	100.0
Deer Killed	N	3	1		6	4	4	9	7	23	19	11	11	98
	%	3.1	1.0		6.1	4.1	4.1	9.2	7.1	23.5	19.4	11.2	11.2	100.0

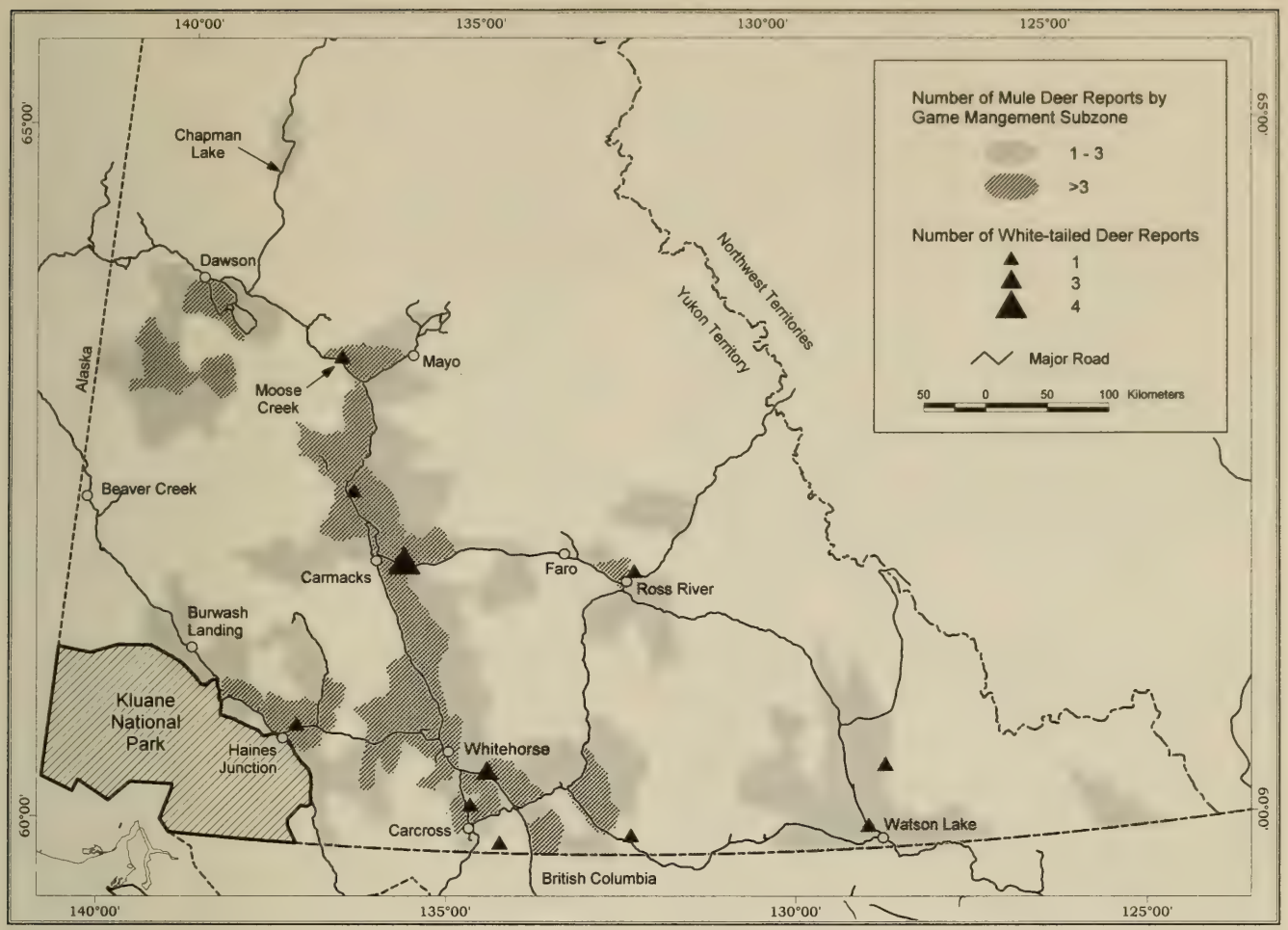

Figure 5. Map showing the distribution of deer sightings. Reported sightings were allocated to game management zones, since many of them were not detailed enough for a more accurate recording of location.

ment is restricted by thick snow, and numbers are then lowest in the annual cycle of births and mortalities. Snow disappears in April and May allowing deer to move about in search for preferred forages and observations and losses thus increase. Most fawns are born in June, but because of the deer's habit of hiding them when they are young, they are not visible until July when they start following their mothers. The annual peak in observations and mortalities is reached in the pre-rut and rutting period (September–November) when deer are very mobile as well as less cautious of humans and traffic.

The range extensions observed in the Yukon have also been reported from neighboring jurisdictions. Mule Deer have been sighted in the Tok area of Alaska since the mid 1980s. Since the deer indigenous to that State are Sitka or Coastal Black-tailed Deer (*Odocoileus hemionus sitkensis*), Mule Deer must have moved into Alaska from the Yukon. The first observations were made near Tok, and the sighting farthest north and west was made in March 1989 near Salcha (Bostian 1989). This location is about 60 km east of Fairbanks along the Tanana River and about 300 km northwest of the Yukon border. Based on the chronology of observations it is assumed that deer crossed into Alaska in the late 1970s to early 1980s following the valley of the Ladue River upstream (Hoefs 2000*). Independent of Mule Deer the Black-tailed Deer have also been observed north of their traditional range in Alaska (Roberson 1986), but these may be temporary dispersals and not permanent range extensions.

In the Northwest Territories both Mule Deer and White-tailed Deer are moving north, but here it is the White-tailed Deer that has made most progress. The first sighting of a White-tailed Deer was reported by Kuyt (1966) from the Fort Smith area, while a Mule Deer had already been reported for the vicinity of Fort Simpson 30 years earlier (Bethune 1937). Scotter (1974) lists a number of observations of both species made between 1955 and 1971 along the South Nahanni River and adjacent areas, which have since become part of Nahanni National Park. Veitch (2001) summarized White-tailed Deer observations from the southwestern N.W.T and neighboring regions and described a record of a White-tailed doe taken by native residents on the MacKenzie River about 100 km south of the Arctic Circle. This represented the northernmost occurrence for this species in North America.

This northward spread of deer in the Yukon and N.W.T. is a continuation of the range extensions reported for British Columbia (Cowan and Guiguet 1965) and the Prairies (Wishart 1984; Gainer 1995). A number of factors have been suggested as possible causes: warming trend in climate, northward spread of agriculture, control of predators, lack of competition from other ungulates, and protection (Wishart 1984; Veitch 2001; Hoefs 2000*).

It is my opinion that this range extension is a predictable and expected post-glacial phenomenon with the factors listed above only serving to accelerate this trend. Much of the Yukon was covered by ice during the Wisconsin glaciation, which lasted until about 12 000 years ago (Valdez 1982). Many of the large mammals indigenous to the Yukon (caribou, thinhorn sheep, grizzly, wolf) had survived the glacial periods in the Beringia refugium, which extended from central Yukon across Alaska into Siberia. These species colonized the glaciated portions of the Yukon relative quickly, because they were already in the region and simply had to invade newly developing habitat in the wake of retreating glaciers. Deer, on the other hand, along with other large mammals such as cougar, elk and coyote, survived the glacial periods south of the continental ice sheets in what is now the United States. They had to colonize all of eastern British Columbia and western Alberta first, before reaching theYukon border.

The deer's colonization of the Yukon is a post-glacial trend also seen in other mammals, birds and plants that reflects the youthful status of this Territory in the context of faunal and floral evolution (Hoefs 2000*). A balance between current species assemblages with environmental conditions as seen in more southern regions has not yet been reached. No doubt warmer winters in recent decades, widespread wolf controls in the 1950s to 1970s, and the status of deer as an endangered species under the Yukon Act, protecting them from subsistence hunting, has accelerated the deer's range expansion across the Yukon.

Acknowledgments

Thanks are due to many members of the public, conservation officers, biologists, and staff of highway maintenance camps, who have contributed most of the sight records and information on deer mortalities in traffic collisions, on which this report is based. Marcus Waterreus drafted the figures and Stuart Alexander applied his GIS expertise to generate the map. To all these contributors I extend my most sincere gratitude.

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New Records of Vascular Plants in the Yukon Territory III

WILLIAM J. CODY[1], CATHERINE E. KENNEDY[2] AND BRUCE BENNETT[2]

[1]Biological Resources Program, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Central Experimental Farm, Ottawa, Ontario K1A 0C6, Canada
[2]Department of Renewable Resources, Government of the Yukon, Box 2703, Whitehorse, Yukon Y1A 2C6, Canada

Cody, William J., Catherine E. Kennedy, and Bruce Bennett. 2001. New records of vascular plants in the Yukon Territory III. Canadian Field-Naturalist 115(2): 301–322.

Ten native taxa including *Arabis boivinii, Carex aquatilis* ssp. *stans, Descurainia incisa* var. *incisa, Draba lonchocarpa* var. *vestita, Isoetes maritima, Lepidium densiflorum* var. *macrocarpum, Malaxis paludosa, Phyllodoce* × *intermedia, Scirpus acutus, Stipa hymenoides* and *Taraxacum carneocoloratum* are reported new to the known flora of the Yukon Territory. Three introduced taxa including *Centaurea cyanus, Lolium perenne* ssp. *multiflorum, Rheum rhaponticum* and *Sorbaria sorbifolia* are also reported as new to the known flora. Significant range extensions within the Territory are reported for 127 native and 21 introduced taxa and comments are presented on four native taxa. Of these, 10 native and three introduced are new for the Territory. The total vascular flora is now 1163 species.

Key Words: Vascular flora, range extensions, Yukon Territory.

Since the writing of *New Records of Vascular Plants in the Yukon Territory II* (Cody et al. 2000), a considerable number of plant specimens have been submitted to Cody for identification and confirmation, in particular those from: Bruce Bennett, while working for Yukon Department of Renewable Resources as a wildlife viewing biologist and volunteering on other projects in various areas in southern Yukon; Greg Brunner, while working with a survey party in the Peel River wetlands area in northeastern Yukon; and John Meikle while cruising down the Snake River near the Mackenzie-Northwest Territory border. In addition, Cody spent five weeks in 1999 in the Territory which included two weeks with his son Gordon surveying flora along the highways in the southern part of the Territory, a week with Kennedy and Scott Smith studying the vegetation of Herschel Island and three days examining the vegetation in the northern portion of proposed Tombstone territorial park in the Ogilvie Mountains also with Kennedy and Scott Smith.

This paper, along with other additional records recently published (Cody et al. 1998, 2000) further updates *the Flora of the Yukon Territory* (Cody 1996) and *Flora of the Yukon Territory, Second Edition* (Cody 2000). The floristic information presented earlier and updated here is essential for biological research and ongoing work relating to agriculture, forestry, sustainable resource management and wildlife management. With additions of ten native and three introduced species reported here the flora now includes 1163 species. The new native species are all rare (as defined by Douglas et al. 1981) in the Territory.

The taxa in this paper appear first in a synoptic list by Yukon status in alphabetical order. The taxa are then discussed in taxonomic order, as presented in the *Flora of the Yukon Territory* with citation of specimens and other pertinent information. Common names follow Cody (1996) and Douglas et al. (1984, 1990, 1991, 1994). Most of the specimens which were sent to the senior author for identification and verification have been incorporated into the vascular plant herbarium maintained by Agriculture and Agri-Food Canada at the Central Experimental Farm, Ottawa (DAO). Those not retained were photographed and the photographs have been preserved in DAO.

Synoptic List by Yukon Status

Errata in *New Records of Vascular Plants in the Yukon Territory II*: (2)

Cerastium nutans
Draba densifolia

Native taxa new to the Yukon Territory: (10)

Arabis boivinii
Descurainia incisa var. *incisa*
Draba lonchocarpa var. *vestita*
Isoetes maritima
Lepidium densiflorum var. *macrocarpum*
Malaxis paludosa
Phyllodoce × *intermedia*
Scirpus acutus
Stipa hymenoides
Taraxacum carneocoloratum

Introduced taxa new to the Yukon Territory: (3)

Centaurea cyanus
Rheum rhaponticum
Sorbaria sorbifolia

Range extensions of native taxa within the Yukon Territory: (127)

Androsace septentrionalis
Angelica lucida
Antennaria densifolia

Antennaria pulcherrima
Artemisia michauxiana
Artemisia tilesii
Arabis drummondii
Arabis holboellii var. *retrofracta*
Arabis holboellii var. *secunda*
Arabis nuttallii
Arctophila fulva
Astragalus adsurgens ssp. *robustior*
Boykinia richardsonii
Braya humilis
Carex aenea
Carex albo-nigra
Carex aquatilis ssp. *stans*
Carex atratiformis ssp. *raymondii*
Carex atrofusca
Carex aurea
Carex bicolor
Carex capillaris ssp. *capillaris*
Carex capillaris ssp. *robustior*
Carex chordorrhiza
Carex crawfordii
Carex diandra
Carex lachenalii
Carex livida
Carex obtusata
Carex rariflora
Carex stylosa
Carex tenuiflora
Cassiope tetragona ssp. *saximontana*
Castilleja caudata
Castilleja miniata
Castilleja raupii
Castilleja yukonis
Cicuta virosa
Coeloglossum viride ssp. *bracteatum*
Crepis elegans
Cryptogramma stelleri
Descurainia pinnata ssp. *nelsonii*
Descurainia sophioides
Draba borealis
Draba cinerea
Draba nemorosa var. *leiocarpa*
Draba scotteri
Draba stenopetala
Elymus trachycaulus ssp. *subsecundus*
Equisetum arvense
Equisetum scirpoides
Equisetum variegatum ssp. *variegatum*
Erigeron acris ssp. *politus*
Erigeron elatus
Eriophorum gracile
Eriophorum russeolum var. *albidum*
Geum aleppicum ssp. *strictum*
Juncus bufonius
Kalmia polifolia
Limosella aquatica
Lycopodium clavatum var. *monostachyon*
Maianthemum trifolium
Mentha arvensis
Minuartia biflora
Moehringia lateriflora
Montia fontana
Myrica gale
Oxytropis campestris ssp. *jordalii*
Oxytropis deflexa ssp. *foliolosa*
Oxytropis deflexa ssp. *sericea*
Oxytropis scammaniana
Parrya arctica
Pedicularis macrodonta
Pedicularis verticillata
Petasites frigidus ssp. *frigidus*
Phalaris arundinacea
Pinguicula vulgaris ssp. *vulgaris*
Platanthera aquilonis (*P. hyperborea*)
Platanthera obtusata
Polygonum alaskanum
Polygonum viviparum
Potamogeton alpinus ssp. *tenuifolius*
Potamogeton foliosus var. *macellus*
Potamogeton richardsonii
Potamogeton zosteriformis
Potentilla norvegica
Potentilla rubricaulis
Puccinellia andersonii
Pyrola minor
Ranunculus hyperboreus
Rhodiola rosea ssp. *integrifolia*
Rorippa palustris
Rubus chamaemorus
Rubus pubescens
Rumex acetosa ssp. *alpestris*
Rumex salicifolius ssp. *triangulivalvis*
Sagina saginoides
Salix alaxensis ssp. *longistylis*
Salix arctophila
Salix barrattiana
Salix pedicellaris
Salix pyrifolia
Saxifraga adscendens ssp. *oregonensis*
Saxifraga aizoides
Saxifraga bronchialis ssp. *funstonii*
Scheuchzeria palustris ssp. *americana*
Scirpus caespitosus ssp. *austriacus*
Scirpus rollandii
Selaginella selaginoides
Senecio hyperborealis
Senecio lugens
Silene uralensis ssp. *ogilviensis*
Sparganium minimum
Sparganium multipedunculatum
Spiranthes romanzoffiana
Stellaria longipes
Stipa nelsonii ssp. *dorei*
Thalictrum alpinum
Tofieldia coccinea
Tofieldia glutinosa ssp. *brevistyla*
Tofieldia pusilla
Triglochin maritimum
Typha latifolia
Utricularia intermedia
Utricularia vulgaris ssp. *macrorhiza*
Woodsia glabella

Range extensions of introduced taxa within the Yukon Territory: (21)

Alopecurus pratensis
Astragalus cicer
Caragana arborescens
Clematis tangutica

Crepis tectorum
Elymus repens
Galeopsis tetrahit ssp. *bifida*
Hordeum brachyantherum
Lepidium ramosissimum
Lolium perenne ssp. *multiflorum*
Medicago falcata
Medicago sativa
Melilotus alba
Melilotus officinalis
Polygonum buxiforme
Polygonum lapathifolium
Sonchus arvensis ssp. *uliginosus*
Stellaria media
Taraxacum officinale
Thlaspi arvense
Vicia cracca

Comments on native taxa in the Yukon Territory: (5)

Adoxa moschatellina
Isoetes echinospora
Platanthera aquilonis
Poa cusickii
Scirpus validus

Taxonomic List

LYCOPODIACEAE

Lycopodium clavatum L. var. *monostachyon* Hook. & Grev., Common Club-moss – YUKON: alpine dry ridge above talus steep rocky slope, Beavercrow Ridge, 60°14'N 124°32'W, B. Bennett 98-366, 15 Aug. 1998 (DAO).

The specimen cited above is an extension of the known range in the Yukon Territory of about 180 kilometers from a site west of longitude 127°W (Cody 1996).

SELAGINELLACEAE

Selaginella selaginoides (L.) Link, Northern Selaginella – YUKON: rich tall willow site, middle of Seela Pass, Tombstone Range, Ogilvie Mountains, 64°42.58'N 139°51.304'W, *W. J. Cody 36401*, 20-22 July 1999 (DAO).

Cody (1996) knew this species in the Yukon Territory mainly from south of latitude 62°N and then disjunct to the northern end of the Canol Road and two sites north of latitude 64°N east of the Dempster Highway. The specimen cited above is an extension of the known range to the west of about 75 kilometers from the northernmost site adjacent to the Dempster Highway.

ISOETACEAE

Isoetes echinospora Dur.

The northern dot on the distribution map of this species in the *Flora of the Yukon* (Cody 1996) should be removed. The specimen on which it was based has been revised to *I. maritima* – see below.

Isoetes maritima Underw., Maritime Quillwort – YUKON: in shallow water, south end of Sheldon Lake, opposite Mile 219 Canol Road, *Porsild & Breitung 11502*, 17 Aug. 1944 (CAN); fen, Peel River Wetland Study, Vittrewka Lake, 66°49'7.41"N 135°31'8.93"W, *G. Brunner 39-99*, 29 June 1999 (Yukon Renewable Resources, DAO) (determined by D. M. Britton).

Porsild (1951) originally determined the first specimen as *Isoetes braunii* (*I. echinospora* Dur.). Brunton and Britton (1999) revised it to *I. maritima*. The second specimen is an extension to the known range in the Yukon Territory of about 575 kilometers to the northwest. Brunton and Britton published the following information:

"Origin and dispersal

At their closest, contemporary populations of *Isoetes maritima* in coastal southern Alaska are separated by ca. 500 km and across several mountain ranges from the Sheldon Lake population and are not connected to it by river systems. Disjunct interior British Columbia *I. maritima*, on the other hand, is less than 200 km from the species' primary coastal range and is connected directly to those populations by major river systems (Britton and Brunton 1995). The apparently isolated populations in the Fairbanks areas of eastern interior Alaska are over 900 km west of the Sheldon Lake population but occur within the same drainage system, the Yukon River.

Much of the Yukon River watershed was unglaciated during the Wisconsinan glaciation when the Cordilleran and Laurentide ice sheets covered much of northern North America (Dyke and Prest 1987). The unglaciated corridor across the Yukon River watershed constituted the eastern portion of Beringia, serving both as a glacial era refugium and a post-glacial floristic and faunal migration corridor (Hultén 1968; Schweger 1989). The Alaska-British Columbia coastal band along which *Isoetes maritima* is common today, however, as well as the intervening interior mountains, continued to be covered in glacial ice sheets during this time (Hughes et al. 1989)."

Isoetes maritima can be separated from *I. echinospora* as follows:

A. Spines on megaspores long and acute, not reduced in size near the equator; microspores smooth or with very fine thread-like spines *I. echinospora*

A[1]. Spines on megaspores blunt, sometimes confluent into ridges, reduced to small tubercules near equator; microspores echinate with coarse pronounced spines *I. maritima*

Isoetes maritima should be added to the list of rare plants in the Yukon Territory (Douglas et al. 1981).

EQUISETACEAE

Equisetum arvense L., Field Horsetail – YUKON: edge of active floodplain in poorly developed soil amongst leaf litter, Snake River, 64°57.16'N 133°00.21'W, *J. Meikle 99-001*, 19 July 1999 (Yukon Renewable Resources, photo DAO); Snake River, 65°56'N 133°17'W, *J. Meikle 99-002*, 22 July 1999 (Yukon Renewable Resources, photo DAO).

This species has not previously been recorded from the Snake River area in the Yukon Territory. The specimens cited above are about 100 kilometers from sites mapped by Cody (1996).

Equisetum scirpoides Michx., Dwarf Scouring-rush – YUKON: growing in feathermoss in white spruce valley forest, Snake River, 64°57.16'N 133°00.25'W, *J. Meikle 003*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

This species, which is common in the Yukon Territory

(Cody 1996) was not previously known from the Snake River area where it was collected on a site about 150 kilometers northeast from the vicinity of Mayo.

Equisetum variegatum Schleich. ssp. *variegatum*, Variegated Horsetail – YUKON: poorly developed soil at edge of active flood plain; in willow leaf litter at forest edge, Snake River, 64°57.16'N 133°00.21'W, *J. Meikle 99-004*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

This species is widespread in the Yukon Territory (Cody 1996). The specimen cited above from the Snake River area is an extension of the known range in the Territory of about 100 kilometers northeast of a site in the Wernecke Mountains (Cody 1996).

PTERIDACEAE

Cryptogramma stelleri (Gmel.) Prantl, Slender Cliff-brake – YUKON: SW facing slope, small carbonate face 70-100 m above river about 1 km downstream from lower South Bend on east side of river, Snake River, 65°06.5'N 133°07'W, *J. Meikle 99-005*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

Douglas et al. (1981) considered this species rare in the Yukon Territory. The nearest sites known to Cody (1996) to the specimen cited above were from about 240 kilometers to the west adjacent to the Dempster Highway.

ASPIDIACEAE

Woodsia glabella R.Br., Smooth Woodsia – YUKON: SW facing slope, small carbonate face 70-100 m above river about 1 km downstream from lower South Bend on east side of river, Snake River, 65°06.5'N 133°07'W, *J. Meikle 99-006*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of approximately 115 kilometers northeast of a site in the Wernecke Mountains in the Yukon Territory (Cody 1996).

TYPHACEAE

Typha latifolia L., Common Cattail – YUKON: large patches, Faro Sewage Ponds, 60°13'N 133°22'W, *B. Bennett 99-561*, 28 Oct. 1999 (DAO).

The specimen cited above is only the third known locality in the Yukon Territory; it is intermediate between a site in the vicinity of Mayo (Douglas et al. 1981) and a site in the extreme southeast (Cody et al. 2000).

SPARGANIACEAE

Sparganium minimum (Hartm.) Fries, Small Burreed – YUKON: Turner Lake, 66°09'56"N 134°17'16"W, *G. Brunner 52-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO); No Gold Creek, Horseshoe Slough, 63°26'N 135°06'W, *D. Mossop s.n.*, 1 July 1999 (B. Bennett Herbarium, photo DAO).

Cody (1996) knew this rare species from only three sites in the Yukon Territory. Cody et al. (1998, 2000) added additional sites in the southeast in the vicinities of the La Biche River, Liard Plateau and Upper Coal River. The specimens cited above are extensions of the known range to the northeast of about 350 kilometers from the vicinity of Dawson and 200 kilometers southeast of Dawson.

Sparganium multipedunculatum (Morong) Rydb. – YUKON: small pond by South McQuesten River near Elsa, 63°56.2'N 135°34.4'W, *S. Withers 528*, 10 Aug. 1999 (DAO).

This species, although not frequent in the Yukon Territory, was not included in the rare plants of the Territory because it is widespread to the south. Cody et al. (1998, 2000) added new records in the southeast from the vicinities of Frances Lake and Beaver River. The specimen cited above is from a location about 150 kilometers east of a site south of the south end of the Dempster Highway and 200 kilometers north of Carmacks (Cody 1996).

POTAMOGETONACEAE

Potamogeton alpinus Balbis ssp. *tenuifolius* (Raf.) Hultén, Pondweed – YUKON: Turner Lake, *G. Brunner 41-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range of about 230 kilometers to the northeast of locations adjacent to the Dempster Highway and 280 kilometers to the southeast from a site north of the Porcupine River mapped by Cody (1996).

Potamogeton foliosus Raf. var. *macellus* Fern., Closed-leaved Pondweed – YUKON: in pools below hotsprings, Beaver River Hotsprings, 60°22.53'N 125°34.33'W, *B. Bennett 98-603*, 14 Aug. 1998 (DAO).

This is a rare species in the Yukon Territory (Douglas et al. 1981) where Cody (1996) knew it from only five sites, all west of longitude 135°W. The specimen cited above is from a site about 675 kilometers to the southeast.

Potamogeton richardsonii (Benn.) Rydb., Richardson's Pondweed – YUKON: fen, Turner Lake, 66°10'30.71"N 134°14'49.04"W, *G. Brunner 42-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO); shallow water, Taber Lake, 66°58'42.26"N 134°46'55.51"W, *G. Brunner 1-99* (Yukon Renewable Resources, photo DAO).

Specimens mapped by Cody (1996) were north to about latitude 64°50'N adjacent to the Dempster Highway and disjunct to north of the Porcupine River. The specimens cited above are from the easterly part of the intermittent area.

Potamogeton zosteriformis Fern., Eel-grass Pondweed – YUKON: Nordenskiold River area, 60°41.8'N 131°47.22'W, *M. Dennington 28*, 14 Aug. 1984 (DAO).

Cody (1994, 1996) knew this rare species in the Yukon Territory from only two localities west of longitude 135°W. Cody et al. (1998) extended the known range in the Territory to the Old Crow Flats north of latitude 68°N and Cody et al. (2000) reported an additional locality in the extreme southeast in the Beaver River area. The specimen cited above is from a site intermediate between the Beaver River site and a site southeast of Haines Junction.

SCHEUCHZERIACEAE

Scheuchzeria palustris L. ssp. *americana* (Fern.) Hultén, Scheuchzeria – YUKON: fen, Turner Lake, 66°10'30.71"N 134°14'49.04"W, *G. Brunner 43-99*,

2 July 1999 (Yukon Renewable Resources, photo DAO); fen, Taber Lake, 66°56'29.96"N 134°43'48.30"W, *G. Brunner 9-99*, 25 June 1999 (Yukon Renewable Resources, photo DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory only in the Mayo area. Cody (1996) plotted an additional location to the south in the Pelly River area and Cody et al. (1998) recorded two additional sites in the Frances Lake and Watson Lake areas. The specimens cited above extend the known range in the Territory about 350 kilometers north from the Mayo area.

Triglochin maritimum L. Seaside Arrow-grass – YUKON: Turner Lake, 66°10'30.71"N 134°14'49.04"W, *G. Brunner 45-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 180 kilometers northeast of a site adjacent to the Dempster Highway and of about 250 kilometers to the southeast of a site north of the Porcupine River.

POACEAE (GRAMINEAE)

Alopecurus pratensis L., Meadow Foxtail – YUKON: reclaimed mining trench, Red Ridge, 60°21.5'N 135°04.2'W, *S. Withers 99-106*, 14 July 1999 (B. Bennett Herbarium, photo DAO); white flats below Elsa, 63°55'N 135°29'W, *Cody & Cody 35786*, 4 July 1999 (DAO).

Cody (1996) knew this introduced species in the Yukon Territory from only three locations: Dawson, south of Haines Junction and northwest of Ross River.

Arctophila fulva (Trin.) Rupr., Pendantgrass – Vittrewka Lake, 66°49'57.54"N 135°29'10.81"W, *G. Brunner 24-99*, 27 June 1999 (Yukon Renewable Resources, photo DAO).

This species is widespread in the Yukon Territory (Cody 1996) but was previously unknown from the Eagle Plains between about latitude 65°N adjacent to the Dempster Highway and the Porcupine River.

Elymus repens (L.) Gould, Quack Grass – YUKON: disturbed roadside, Robert Campbell Highway, Km 467, *B. Bennett 99-542*, 19 Aug. 1999 (DAO); roadside between La Biche and Liard River, 60°03'06"N 123°59'35"W, *B. Bennett 95-237*, 15 June 1995 (B. Bennett Herbarium); La Biche Airstrip, 60°07'42"N 124°02'21"W, *B. Bennett 98-581*, 21 June 1998 (DAO).

This introduced species was known in the Yukon Territory (Cody 1996) from the vicinities of Dawson, near the southern end of the Dempster Highway and near Mayo. The specimens cited extend the known range about 750 kilometers to the southeast of Mayo.

Elymus trachycaulus (Link) Gould ssp. *subsecundus* (Link) Gould – YUKON: eroding riverbank, Upper La Biche River, 60°13'58"N 124°13'58"W, *B. Bennett 98-093*, 18 June 1998 (DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 475 kilometers east from sites adjacent to the Canol and Tagish Highways.

Hordeum brachyantherum Nevski, Meadow Barley – YUKON: little silty island in centre of pond, Paddy's Pond, Hillcrest, Whitehorse [60°43'N 135°03'W], *B. Bennett 99-001*, 2 May 1999 (DAO); single patch along lakeshore, Schwatka Lake, Whitehorse, 60°41.45'N 135°02.4'W, *B. Bennett 99-549*, 27 Aug. 1999 (DAO).

This species was previously known in the Yukon Territory (Cody 1996) from only two localities: Carcross, where it was collected by J. M. Gillett in 1949 and considered native, and Dawson where it was collected by Baum and Bailey in 1977 and considered introduced. From the habitat of the specimens cited above, it is probably introduced. The history of Paddy's Pond is that the surface materials were bulldozed off during World War II for fill. Schwatka Lake is a reservoir for the Whitehorse Rapids Dam, and the lakeshore is completely unnatural.

Lolium perenne L. ssp. *multiflorum* (Lam.) Husnot, Italian Rye Grass – YUKON: reclaimed mining trench, Division Mountain near Nordenskiold River, 61°19'N 136°3.5'W, *S. Withers 309*, 26 July 1999 (DAO); adjacent to old railway track at foot of steep clay slope, Whitehorse, 60°42'14.4"N 135°03'10.8"W, *Cody & Cody 37443*, 1 Aug. 2000 (DAO) (determined by S. Darbyshire).

Cody (1996) knew this introduced taxon from only three localities: Dawson, Pelly River Ranch, and east of Watson Lake. The first specimen cited above is from about 100 kilometers southeast of the Pelly River Ranch area. The second specimen is from about 100 kilometers further southeast.

Phalaris arundinacea L., Reed Canary Grass – YUKON: reclaimed mining trench, Mechanic Creek, Big Creek Drainage, 62°20'N 137°19.5'W, *S. Withers 203*, 21 July 1999 (DAO).

Douglas et al. (1981) considered this species rare in the Yukon Territory. The specimen cited above is from an area about 125 kilometers northwest of a site adjacent to the Klondike Highway mapped by Cody (1996) but was germinated from an experimental agronomic seed mix planted in 1995 which included *Phalaris arundinacea*.

Poa cusickii Vasey, Cusick's Bluegrass – YUKON: *Artemisia* – graminoid meadow on glacial till adjacent to Carcross Dunes, rare, 60°10'N 132°42'W, *C. Parker & B. Bennett 8271*, 29 Aug. 1998 (DAO).

Douglas et al. (1981) considered a collection from northwest of Haines Junction near Bear Creek to be an introduction; however, Cody (1994) stated that specimens collected by R. Florkiewicz adjacent to Stony Creek, west of Whitehorse supported the possibility that this species was native in the Yukon Territory. The specimen cited above would also appear to be native in this region.

Puccinellia andersonii Swallen – YUKON: gravel shoreline and adjacent vegetation, Pauline Cove Settlement on Simpson Point, Herschel Island, 69°34'N 138°55'W, *W. J. Cody 36002*, 13 July 1999 (DAO).

This species was known to Cody (1996) in the Yukon Territory from only two sites on the arctic mainland coast.

Stipa hymenoides Roem. & Schult. (*Oryzopsis hymenoides* (Roem. & Schult.) Ricker, *Achnatherum hymenoides* (Roem. & Schult.) Barkworth), Indian Ricegrass (Figure 1) – YUKON: widespread on sandy eroding slope beside hydro dam growing with *Stipa comata*, *Elymus calderi* and *Penstemon gormanii*, Schwatka Lake Dam, Whitehorse, 60°41.75'N 135°02.34'W, *B. Bennett 99-499*, 26 Aug. 1999 (DAO, B. Bennett Herbarium).

This is a North American species, which is common in southcentral and southeastern British Columbia and is found eastward to southwestern Manitoba and south to Texas, New Mexico, Arizona, California and Mexico. It is new to the Yukon Territory and may be introduced in this area because it is adjacent to the old tramway which passed by the Whitehorse Rapids. It is, however, growing beside species which are endemic or rare in the Yukon. Its assocation with a natural habitat suggests that it is native and there is a precedent for widespread southern prairie species on south-facing slopes in the Yukon Territory. *Stipa hymenoides* may be separated from *S. richardsonii* as follows:

A. Awns 16-60 mm long, persistent; lemmas 5-6 mm long, pubescent with hairs about 1 mm long *S. richardsonii*

A[1]. Awns 3-6 mm long, deciduous; lemmas subglobose to fusiform, 2.5-5.0 mm long, pubescent with hairs to 6 mm long *S. hymenoides*

Stipa nelsonii Scribn. ssp. *dorei* Barkworth & Maze, Columbian Needlegrass – YUKON: stabilized dunes, Carcross Dunes, 60°10.35'N 134°43.26'W, *B. Bennett 99-355*, 27 Aug. 1999 (DAO).

Cody (1996) knew this species from only six locations in southern Yukon Territory. At the site reported above over 50 plants were observed.

CYPERACEAE

Carex aenea Fern., Bronze Sedge – YUKON: sandy silt riverbank, La Biche River, 60°13'58"N 124°13'58"W, *B. Bennett 98-113*, 17 June 1998 (DAO).

Cody (1996) knew this species in the Yukon Territory from scattered localities north to latitude 64°N. The specimen cited above is an extension of the known range in the Territory of about 275 kilometers east of Watson Lake.

Carex albo-nigra Mack., Two-toned Sedge – YUKON: in rock crack of dolomite bedrock on exposed ledge on edge of ridge, Beavercrow Ridge, 60°12.41'N 124°35.99'W, *B. Bennett 98-630*, 16 Aug. 1998 (DAO).

This species which was considered rare in the Yukon Territory by Douglas et al. (1981) was known to Cody (1996) as far north as latitude 62°30'N. The specimen cited above is an extension of the known range of about 280 kilometers east of a site west of Watson Lake.

Carex aquatilis Wahlenb. ssp. *stans* (Drej.) Hultén – YUKON: wet mesic flats, SW shore of outer Delta, Phillips Bay, 69°14'N 138°29'W, *Dickson & Allen 5353*, 28 July 1982 (DAO).

Hultén (1968) mapped several Yukon Territory specimens under this high arctic subspecies but Cody (1996) included them in his treatment of ssp. *aquatilis*. Cody et al. (1998) reported a collection of ssp. *stans* from Stokes Point Lagoon. The specimen cited above is the second record from this area.

Carex atratiformis Britt. ssp. *raymondii* (Calder) A. E. Porsild, Black Sedge – YUKON: high subalpine scree, Kotaneelee Range, 60°14'N 124°07'W, *B. Bennett & R. Rosie 98-345*, 19 June 1998 (B. Bennett Herbarium, photo DAO).

Cody et al. (2000) extended the known range of this taxon in the Yukon Territory about 200 kilometers southeast from Frances Lake to the Beaver River area. The specimen cited above is a further extension of about 125 kilometers to the southeast.

FIGURE 1. *Stipa hymenoides* (Drawn by Lee Mennell).

Carex atrofusca Schk. – YUKON: subalpine moist herb meadow, Kotaneelee Range, 60°14.31'N 124°07.19'W, *B. Bennett 98-058*, 20 June 1998 (DAO).

Cody et al. (2000) extended the known range in the Yukon Territory of this circumboreal species (which was not included in the rare plants of the Territory, Douglas et al. 1981) to the headwaters of the Bonnet Plume River. The specimen cited above is an extension of the known range of about 400 kilometers eastward from a site adjacent to longitude 131°W.

Carex aurea Nutt., Golden Sedge, Snake River, 65°12.32'N 133°19.70'W, *J. Meikle 96-007*, 20 July 1999 (Yukon Renewable Resources, photo DAO); riverbar, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-748*, 2 July 2000 (DAO).

The specimens cited above are an extension of the known range in the Yukon Territory (Cody 1996) of about 225 kilometers northeast of a site near Mayo and east of a site adjacent to the Dempster Highway.

Carex bicolor All., Two-coloured Sedge – YUKON: *Salix brachycarpa-Carex parryana* community, Slim's River Delta, 60°59.6'N 138°29.4'W, *S. Withers 38B*, 7 July 1999 (DAO).

Cody (1996) considered this species rare south of latitude 63°30'N in the Yukon Territory. The specimen cited above is from about 75 kilometers southeast of a site in Kluane National Park.

Carex capillaris L. ssp. *capillaris*, Hairlike Sedge – YUKON: fen, Taber Lake, 66°59'40.22"N 134°44'51.14"W, *G. Brunner 5-99*, 24 June 1999 (Yukon Renewable Resources, photo DAO); swamp, Vittrewka Lake, 66°49'19.23"N 135°29'45.93"W, *G. Brunner 22-99*, 27 June 1999 (Yukon Renewable Resources, photo DAO).

The specimens cited above are from sites about 70 kilometers east and northeast of sites mapped by Cody (1996) east of the Dempster Highway.

Carex capillaris L. ssp. *robustior* (Drej. ex Lange) Böcher, Hairlike Sedge – YUKON: marl area near McLean Creek south of Whitehorse, 60°35'N 134°55'W, *Cody & Cody 35638*, 27 June 1999 (DAO).

This subspecies was widely scattered in the Yukon Territory west of longitude 137°W according to Cody (1996). The specimen cited above is an extension eastward from Kluane National Park of about 140 kilometers.

Carex chordorrhiza Ehrh. ex L.f., Cordroot Sedge – YUKON: fen, Turner Lake, 66°10'43.25"N 134°14'37.37"W, *G. Brunner 60-99*, 1 July 1999 (Yukon Renewable Resources, DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 225 kilometers northwest of a site adjacent to the Dempster Highway and 240 kilometers southwest of sites adjacent to the Porcupine River.

Carex crawfordii Fern., Crawford's Sedge – YUKON: old road to wetland west of bridge, La Biche River, 60°05.74'N 124°01.98'W, *B. Bennett 98-634*, 15 June 1998 (DAO).

Douglas et al. (1981) considered this species rare in the Yukon Territory. The specimen cited above is an extension of the known range in the Territory of about 180 kilometers to the east of the easternmost site mapped by Cody (1996).

Carex diandra Schrank, Lesser Panicled Sedge – YUKON: Turner Lake, 66°09'56.9"N 134°17'16.6"W, *G. Brunner 53-99*, 1 July 1999 (Yukon Renewable Resources, DAO).

The nearest sites of this species mapped by Cody (1996) were from the vicinity of Dawson about 325 kilometers to the southwest and adjacent to the Porcupine River about 285 kilometers to the northwest.

Carex lachenalii Schk., Two-parted Sedge – YUKON: subalpine *Salix/Abies* adjacent to *Carex* meadow in draw, Beavercrow Ridge, 60°12.865'N 124°35.79'W, *B. Bennett 98-631*, 16 Aug. 1998 (DAO).

Cody et al. (1998) extended the known range of this species into the southeast of the Yukon Territory. The specimen cited above is a further extension of the range in the southeast of about 175 kilometers.

Carex livida Willd., Livid Sedge – YUKON: fen, Turner Lake, 66°10'43.25"N 134°14'37.37"W, *G. Brunner 55-99*, 1 July 1999 (Yukon Renewable Resources, DAO).

The nearest site of this rare species in the Yukon Territory known to Cody (1996) was adjacent to the Dempster Highway, about 200 kilometers to the southwest of the specimen cited above.

Carex obtusata Liljeb., Blunt Sedge – YUKON: Herschel Island, near Pauline Cove Settlement, 69°34'N 138°55'W, *W. J. Cody & C. E. Kennedy 36351*, 18 July 1999 (DAO).

In the Yukon Territory this species was known to Cody (1996) in the south from the South Canol Road to the west and north to about 64°15'N and then rare north to the Arctic Coast. The specimen cited above is new to Herschel Island and the nearest collection by C. Cain in 1962 was found on a lushly vegetated bench on plain back from the mainland coast at about 138°10'W near King Point (DAO).

Carex rariflora (Wahlenb.) Sm., Loose-flower Alpine Sedge – YUKON: bog, Vittrewka Lake, 66°49'4.94"N 135°30'48.84"W, *G. Brunner 37-99*, 29 June 1999 (Yukon Renewable Resources, photo DAO).

This species, which was considered to be rare in the Yukon Territory in the extreme northeast and adjacent to the Dempster Highway by Douglas et al. (1981) was shown to be much more widespread north of the Porcupine River by Cody (1996). The specimen cited above is from a site about 250 kilometers northeast of the northernmost location known adjacent to the Dempster Highway and 80 kilometers south of a site adjacent to the Rat River.

Carex stylosa C. A. Mey., Long-styled Sedge – YUKON: hummocky terrain, White Hat Hills, Tombstone Range, Ogilvie Mountains, 64°45.20'N 138°29.113'W, *W. J. Cody 36484*, 20-22 July 1999 (DAO).

Cody (1996) knew this species which was considered rare in the Yukon Territory (Douglas et al. 1981) only as far north as the vicinity of Dawson. The specimen cited above is an extension of the known range northward of about 60 kilometers from Dawson. Cody et al. (2000) did however report a specimen from the Arctic coast.

Carex tenuiflora Wahlenb., Sparse-leaved Sedge – YUKON: open shrub/*Ledum*/lichen, Vittrewka Lake, 66°49'42.37"N 135°36'10.82"W, *G. Brunner 27-99*, 28 June 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 175 kilometers northeast of a site in the Ogilvie Mountains at 65°48'N 138°35'W and 200 kilometers southeast of the Old Crow region adjacent to the Porcupine River.

Eriophorum gracile Koch, Slender Cotton-grass – YUKON: fen, Turner Lake, 66°11'06.09"N 134°16'45.14"W, *G. Brunner 48-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO).

This is a rare species in the Yukon Territory that was unknown to Douglas et al. (1981). Cody (1994) reported the first collection from the southeast in the Coal River Springs area and Cody et al. (1998) reported two additional sites from the Upper Coal River and Frances Lake areas. The specimen cited above is an extension of the known range of about 630 kilometers northwest from the vicinity of Frances Lake.

Eriophorum russeolum Fries var. *albidum* Nyl. – YUKON: fen, Vittrewka Lake, 66°49'6.56"N 135°30'55.33"W, *G. Brunner 38-99*, 29 June 1999 (Yukon Renewable Resources, photo DAO).

This species is only frequent in the Yukon Territory (Cody 1996) north of latitude 67°N. The specimen cited above from Vittrewka Lake is from about 90 kilometers north of Ursus Lake just north of latitude 66°N.

Scirpus acutus Muhl. (Figure 2, Map 1) – YUKON: specimens from the vicinities of Mayo, Klondike Highway, Ross River and south of Whitehorse treated by Cody (1996) as *S. validus* have been revised to *S. acutus*. These are from the central part of the Yukon Territory south of latitude 64°N. *Scirpus acutus* which is new to the Yukon Territory can be separated from *S. validus* as follows:

A. Fresh culms dark green, firm; aerenchymal lacunae less than 0.9 mm in diameter; inflorescence length usually less than 47 mm; number of primary rays less than 7; secondary rays absent; clusters of 5 or more spikelets present; scales dull, basically pale or whitish brown, the midrib not strongly contrasting, the margins often more copiously ciliate and the backs copiously flecked with shiny red dots, often puberulent; mature achenes ca. 2.2-2.7 mm long, including the apicules, completely hidden by the scales *S. acutus*

A[1]. Fresh culms light green, rather soft; aerenchymal lacunae more than 1.5 mm in diameter; inflorescence length greater than 80 mm; number of primary rays greater than 13; secondary, tertiary, and occasionally quaternary rays present; spikelets mostly borne in clusters 1-3; scales more or less shiny, rich orange-brown, often with prominent greenish midrib, the margins ciliate but

FIGURE 2. *Scirpus acutus* (Drawn by Marcel Jomphe).

MAP 1. *Scirpus acutus*.

the backs essentially glabrous (puberulence and swollen red flecks, if any, limited to the region of midrib); mature (dark gray or lead coloured) achenes ca 1.6-2.1 mm long, including apicules, barely covered by the scales *S. validus*

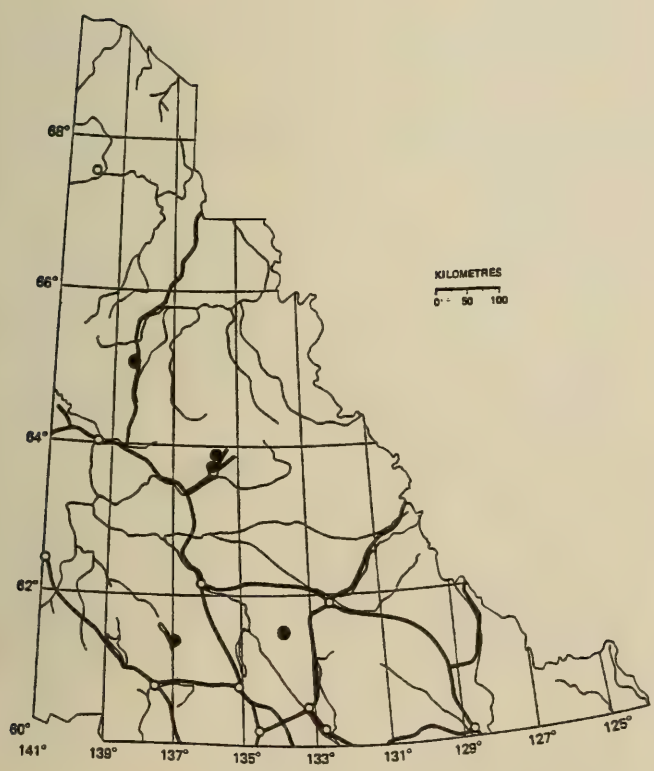
Scirpus caespitosus L. ssp. *austriacus* (Pallas) Asch. & Graeb., Tufted Clubrush – YUKON: swamp, Taber Lake, 66°56'38.65"N 134°44'12.56"W, *G. Brunner 11-99*, 25 June 1999 (Yukon Renewable Resources, photo DAO).

Cody (1996) considered this species in the Yukon Territory as occasional north to the southern part of the Dempster Highway and then disjunct to north of the Porcupine River where it is apparently rare. The specimen cited above from Taber Lake is from the eastern section of the intermediate area.

Scirpus rollandii Fern., (*Trichophorum pumilum* (Vahl) Schinz. & Tehell.), Tufted Clubrush – YUKON: marl lowland near McLean Creek, south of Whitehorse, 60°35'N 134°55'W, *Cody & Cody 35645*, 27 June 1999 (DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory from three localities, all close to Haines Junction. Cody (1996) mapped five sites northwest and east of Haines Junction plus one south of Whitehorse at Watson River at latitude 60°15'N and one north of Whitehorse adjacent to the Twin Lakes at latitude 61°42'N. The new collection cited above is intermediate between Twin Lakes and Watson River areas.

Scirpus validus Vahl, Common Great Bulrush (Map 2) – YUKON: 61°32'N 133°55'W, *C. A. McEwen 6501*, 22 July 1982 (DAO); in wet bog, along Dempster Highway near Mile 92, *R. T. Porsild 1587*, 16 July 1968 (CAN); common locally in very wet bog margins along Dempster Highway near Mile 91, *R. T. Porsild 1752*, 2 Aug. 1968 (CAN); shallow ponds and bogs northeast of Mayo, 63°35'-37'N 135°45'-55'W, *R. T. Porsild 1243*, 28 Aug. 1967 (CAN); artificial wetland, Elsa, 63°55.5'N 135°30.4'W, *S. Withers 521*, 10 Aug. 1999 (DAO); sedge meadow at lake edge, Buffalo Lake, 61°25'22.7"N 137°01'44.19"W, *Staniforth & Rosie 98-77*, 25 Aug. 1998 (DAO).



MAP 2 *Scirpus validus*.

The specimens cited above were treated as *S. validus* by Porsild (1975) and Cody (1996). Other specimens in the Yukon Territory mapped by Cody (1996) have now been revised to *Scirpus acutus* Muhl. (Map 1). *Scirpus validus* is now known from four areas in the Yukon Territory, and should still be considered as rare in the Territory (Douglas et al. 1981).

JUNCACEAE

Juncus bufonius L., Toad Rush – YUKON: in slough off river in silty mud, Upper Wolf River, 60°41.98'N 132°06.62'W, *B. Bennett 99-386*, 13 Aug. 1999 (DAO).

With the exception of a single collection just north of Watson Lake, Cody (1996) knew this species only in central Yukon Territory. Cody et al. (2000) reported an additional site in the extreme southeast in the La Biche River area. The specimen cited above is also from the south, about 180 kilometers west of the Watson Lake collection.

LILIACEAE

Maianthemum trifolium (L.) Sloboda, Three-leaved Solomon's Seal – YUKON: swamp, Turner Lake, 66°10'30.71"N 134°14'49.04"W, *G. Brunner 44-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO); *Sphagnum* bog, Wolf Lake, 60°42.6'N 131°44.08'W, *B. Bennett 99-391*, 11 Aug. 1999 (DAO).

This species was considered rare in the Yukon Territory by Douglas et al. (1981) based on three locations in the southeast. Cody (1996) mapped eight sites in the same general area north to Frances Lake. Cody et al. (1998) reported a site at Enoch Lake north of latitude 68°N and Cody et al. (2000) reported a site south of latitude 66°N. The Turner Lake specimen cited above is from about 70 kilometers northwest of the site south of latitude 66°N; the Wolf Lake site which is the westernmost yet found in the south, is about 100 kilometers northwest of the nearest site mapped by Cody (1996).

Tofieldia coccinea Richards., Northern False Asphodel – YUKON: shallow soil over limestone, Snake River, 65°24'N 133°24'W, *J. Meikle 99-008*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 75 kilometers southeast of a site adjacent to the northern Bonnet Plume River.

Tofieldia glutinosa (Michx.) Pers. ssp. *brevistyla* Hitchc., Sticky False Asphodel – YUKON: fen, Turner Lake, 66°10'1.63"N 134°16'50.66"W, *G.*

Brunner 50-99, 1 July 1999 (Yukon Renewable Resources, photo DAO).

This species was considered rare in the Yukon Territory by Douglas et al. (1981). The specimen cited above is an extension of the known range in the Territory of about 280 kilometers north from Mayo.

Tofieldia pusilla (Michx.) Pers., Common False Asphodel – YUKON: subalpine, moist herb meadow, common, Kotaneelee Range, 60°14'31"N 124°07'19"W, *B. Bennett 98-594* (DAO).

This is a common species throughout most of the Yukon Territory (Cody 1996). The specimen cited above however is an extension of the known range in the southeast of about 200 kilometers east of a site west of longitude 127°W.

ORCHIDACEAE

Coeloglossum viride (L.) Hartm. ssp. *bracteatum* (Muhl.) Hultén – YUKON: sorted gravel with poorly developed soil, Snake River, 65°12.32'N 133°19.70'W, *J. Meikle 99-010*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

This species was considered rare in the Yukon Territory by Douglas et al. (1981). Cody (1996) knew it from only two localities: adjacent to the Bonnet Plume River in the north and Little Atlin Lake in the south. The specimen cited above is from an area about 50 kilometers east of the Bonnet Plume River site.

Malaxis paludosa (L.) Sw. – YUKON: fen, Turner Lake, 66°10'43.25"N 134°14'37.37"W, *G. Brunner 56-99* and *57-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO).

Cody (1996) suggested that this species should be looked for in southern Yukon Territory because it is known in extreme southwestern District of Mackenzie and Alaska (Porsild and Cody 1980; Hultén 1968). It is an extension of the known range northwest of the District of Mackenzie site of about 925 kilometers. *Malaxis paludosa* is a circumpolar species which is apparently rare and local with very large gaps. It should be added to the *Rare Plants of the Yukon Territory* (Douglas et al. 1981).

Platanthera aquilonis Sheviak (*P. hyperborea* (L.) Lindl.), Northern Green Orchid – YUKON: fen, Turner Lake, 66°09'56.9"N 134°17'16.6"W, *G. Brunner 51a-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO); in white spruce forest above active flood plain at lower south bend of river, Snake River, 65°06'N 133°06'W, *J. Meikle 99-014*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

C. J. Sheviah (1999) has recently demonstrated that the name *Platanthera hyperborea* has been misapplied by North American workers and has provided our plant with a new name, *P. aquilonis*. The first specimen cited above is only the second collection from north of latitude 66° in the Yukon Territory (Cody 1996). This one is from about 80 kilometers northeast of a site adjacent to the Bonnet Plume River (Cody et al. 2000). The second specimen is about 115 kilometers southeast of a site adjacent to the northern Bonnet Plume River and northeast of a site in the Wernecke Mountains.

Platanthera obtusata (Pursh) Lindl., Northern Bog Orchid – YUKON: Snake River, 65°01'N 133°07'W, *J. Meikle 90-015*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

This species is frequent throughout much of the Yukon Territory (Cody 1996). The nearest site to the location cited above is about 150 kilometers to the southwest.

Spiranthes romanzoffiana Cham. & Schlecht., Hooded Ladies'-tresses – YUKON: fen, Turner Lake, 66°09'56.9"N 134°17'16.6"W, *G. Brunner 51b-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO); fen, Turner Lake, 66°10'43.25"N 134°14'37.37"W, *G. Brunner 58-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO).

The specimens cited above are an extension of the known range in the Yukon Territory (Cody 1996) of about 125 kilometers east of a site adjacent to the Dempster Highway.

SALICACEAE

Salix alaxensis (Anderss.) Cov. ssp. *longistylis* (Rydb.) Hultén, Feltleaf Willow – YUKON: riverbar with sandy silt, La Biche River, 60°13'58"N 124°13'58"W, *B. Bennett 98-133*, 17 June 1998 (DAO).

This willow is widespread throughout the Yukon Territory. The specimen cited above, however, extends the known range in the Territory into the extreme southeast about 75 kilometers east of a site about longitude 125°30'W mapped by Cody (1996).

Salix arctophila Cockerell, Northern Willow – YUKON: fluvial fan with moss and peat, Ogilvie Mountains, Patrol Range, middle of Seela Pass, 64°04.58'N 139°51.301'W, *W. J. Cody 36367, 36368*, 20-22 July 1999 (DAO) (determined by G. Argus).

Argus (1973) knew this rare willow in the Yukon Territory from only two localities, one on the Arctic coast and the other from the Macmillan Pass area near the Canol Road. Cody (1996) mapped three additional sites on the Arctic coast and two in the northern Richardson Mountains. The specimen cited above is a new record for central Yukon Territory about 415 kilometers southwest of the southernmost site in the Richardson Mountains and about 500 kilometers northwest of Macmillan Pass.

Salix barrattiana Hook., Barratt's Willow – YUKON: alpine meadow, creek bed and adjacent turfy slopes, Richardson Mountains, 66°44'N 135°52'W, *Cody & Ginns 30896*, 8 July 1982 (DAO) (determined by G. Argus).

Cody (1996) knew this cordilleran species in the Yukon Territory as far north as the Ogilvie and Wernecke Mountains and then disjunct to the British Mountains. The specimen cited above, which is from the eastern part of the intermediate area, was unfortunately misidentified as *S. planifolia* ssp. *pulchra* which is a common species in the Richardson Mountains.

Salix pedicellaris Pursh, Bog Willow – YUKON: bog, Jackfish Lake, 66°49'52.98"N 135°50' 48.25"W, *G. Brunner 61-99*, 3 July 1999 (Yukon Renewable Resources, photo DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory only from the vicinity of Watson Lake. Cody et al. (1998) reported new sites from the vicinities of the Beaver River and Frances Lake. The specimen cited above is an extension of the known range in the Territory of about 700 kilometers to the northwest of Frances Lake. To the east in the Mackenzie River valley Porsild and Cody (1980) knew this species only as far north as the vicinity of Fort Norman.

Salix pyrifolia Anderss., Balsam Willow – YUKON: graminoid/forb area, Vittrewka Lake, 66°49'33.48"N 135°28'47.03"W, *G. Brunner 26-99*, 28 June 1999 (Yukon Renewable Resources, photo DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory from a single location at Palmer Lake in the southern Richardson Mountains. Cody (1996) mapped an additional area in the vicinity of Watson Lake and Cody et al. (2000) reported a collection from the Beaver River area in the extreme southeast. The specimen cited above is an extension of the known range in the Territory northwards from the Palmer Lake area of about 80 kilometers.

MYRICACEAE

Myrica gale L., Sweet Gale – YUKON: Turner Lake, 66°09'56"N 134°17'18.31"W, *G. Brunner 54-99*, 1 July 1999 (Yukon Renewable Resources, photo DAO).

Cody (1996) stated that this species was infrequent in the Yukon Territory north to about latitude 65°30'N adjacent to the Dempster Highway. Cody et al. (2000) extended the range further northward to 67°04'N 137°17'W. The specimen cited above is from about 190 kilometers northeast of the Dempster Highway collection.

POLYGONACEAE

Polygonum alaskanum Wight ex Hultén – YUKON: fossil bluff, active fine scree bluff undercut by river, Snake River, 65°56'N 133°17.06'W, *J. Meikle 99-016*, 22 July 1999 (Yukon Renewable Resources, photo DAO).

East of the Dempster Highway, the only site between latitudes 64°N and 66°N known to Cody (1996) was north of the Peel River. The specimen cited above is from a site about 110 kilometers to the east.

Polygonum buxiforme Small, Eastern Knotweed – YUKON: disturbed area near airstrip, La Biche Airstrip, 60°07'42"N 124°02'21"W, *B. Bennett 98-610*, (B. Bennett Herbarium, photo DAO).

Cody et al. (2000) extended the known range of this species in the Yukon Territory eastward from the vicinity of Johnson's Crossing to the vicinity of the Beaver River. The specimen cited above is a further extension of about 60 kilometers to the east where Bruce Bennett suggests that it may be introduced.

Polygonum lapathifolium L., Willow Weed – YUKON: uncommon in silty mud beside beaver pond, Ottertail Creek, west of Mt. Martin, 60°07'N 124°15'20"W, *B. Bennett 98-609*, 16 June 1998 (DAO).

Cody (1996) knew this introduced weedy species in the Yukon Territory only from west of longitude 135°W where infrequent.

Polygonum viviparum L., Alpine Bistort – YUKON: Snake River, 65°01'N 133°07'W, *J. Meikle 99-017*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

This species is widespread throughout the Yukon Territory (Cody 1996). The nearest site in the Territory to the specimen cited above is adjacent to the upper Bonnet Plume River, about 100 kilometers to the southeast.

Rheum rhaponticum L., Rhubarb – YUKON: growing wild around old buildings, Silver City on east side of Kluane Lake, 61°05'N 138°24'W, *Cody & Cody 35685*, 29 June 1999 (DAO).

This cultivated species has not previously been reported growing wild in the Yukon Territory, but Bruce Bennett noted its occurrence on 17 July 1997 at 17 Mile (old town location 61°30'N 134°40'40"W) on the Teslin River.

Rumex acetosa L. ssp. *alpestris* (Scop.) A. Löve, Green Sorrel – YUKON: by creek, Yakamaw Creek watershed east of Angelcomb Peak, Tombstone Range, Ogilvie Mountains, 64°36'N 138°14'W, *W. J. Cody 36822*, 20-22 July 1999 (DAO); ridge, headwaters of Chandindu River, Patrol Range, Ogilvie Mountains, 64°45'N 139°06'W, *W. J. Cody 36544, 36573*, 20-22 July 1999 (DAO).

Cody (1996) knew this rare species in the Yukon Territory from only three widely separated areas: northern Richardson Mountains, west of northern Kluane Lake and southwest of Watson Lake.

Rumex salicifolius Weinm. ssp. *triangulivalvis* Danser, Willow Dock – YUKON: gravel beside building, Keno, 63°55'N 135°18'W, *Cody & Cody 35781*, 4 July 1999 (DAO).

This species has not previously been found in the Mayo area. The nearest previously known localities (Cody 1996) were adjacent to the Klondike Highway about 125 kilometers to the west and in the vicinity of Carmacks about 200 kilometers south- southwest.

PORTULACACEAE

Montia fontana L., Blinks, or Water Chickweed – YUKON: in moist sand at back of beach, Herschel Island, Adavlek Fan, 69°34.5'N 138°15'W, *W. J. Cody 36266*, 17 July 1999 (DAO) (determined by Cody & McNeill).

This is a circumpolar and often widely spaced species which was previously only known in the Yukon Territory from Shingle Point on the Arctic coast (Douglas et al. 1981; Cody 1996). The collection cited above is a new record for Herschel Island and is about 100 kilometers northwest of Shingle Point. It was a small mass of tiny plants recently sprouted from seeds which were still encasing leaves.

CARYOPHYLLACEAE

Cerastium nutans Raf., Nodding Chickweed –
The drawing of this species in Cody et al., *New Records of Vascular Plants in the Yukon Territory II*, Canadian Field-Naturalist 114(3): 430, 2000 was by Lee Mennell, not Valerie Fulford.

Minuartia biflora (L.) Schinz. & Thell., Mountain Sandwort – YUKON: steep rocky slope above

stream, Ogilvie Mountains, Patrol Range, east of Chandindu River, 64°45'N 139°06'W, *W. J. Cody 36602*, 20-22 July 1999 (DAO).

Cody (1996) stated that this species was occasional north to latitude 64°30'N in the Yukon Territory and then disjunct to the Barn Mountains to the north. The specimen cited above is an extension of the known range in the Ogilvie Mountains of about 75 kilometers northwest from a site adjacent to the Dempster Highway.

Moehringia lateriflora (L.) Fenzl, Blunt-leaved Sandwort – YUKON: Snake River, 64°57.16'N 133°00.21'W, *J. Meikle 99-019*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

This species is widespread throughout much of the Yukon Territory (Cody 1996). The nearest site to that cited above, however, is about 200 kilometers to the southwest in the vicinity of Mayo.

Sagina saginoides (L.) Karst, Arctic Pearlwort – YUKON: near junction of Kaskawulsh, Dezadeash and Alsek rivers, 60°30'N-60°45'N 137°45'W-138°W, *A. M. Pearson 69-10*, 30 June 1969 (DAO).

Douglas et al. (1981) did not include this species in *The Rare Plants of the Yukon* because it was "too widely distributed". Cody (1996), however, mapped it from only seven areas in the Territory, the nearest of which was in the vicinity of Haines Junction.

Silene uralensis (Rupr.) Bocquet ssp. *ogilviensis* (A. E. Porsild) Brunton – YUKON: rich tall willow site, middle of Seela Pass, Patrol Range, Ogilvie Mountains, 64°42.58'N 139°51.304'W, *W. J. Cody 36404*, 20-22 July 1999 (DAO); rocky slope, Richardson Mountains, 66°16'N 135°48'W, *Cody & Ginns 30403*, 6 July 1982 (DAO) (determined by J.K. Morton); river bank, Firth River, British Mountains, 68°48'N 140°39'W, *W. J. Cody 27123*, 7 July 1980 (DAO) (determined by J. K. Morton.)

Cody (1996) knew this rare endemic taxon in the Yukon Territory from only two sites adjacent to the Dempster Highway. The first specimen cited above is an extension of the known range of about 80 kilometers to the west southwest. The Richardson Mountains specimen extends the known range in the Territory about 250 kilometers to the northeast while the British Mountains collection extends the known distribution about 430 kilometers to the north.

Stellaria longipes Goldie, Long-stalked Starwort – YUKON: Jasper Canyon, Snake River, 65°12'N 133°19'W, *J. Meikle 99-020*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

This is a common species throughout much of the Yukon Territory (Cody 1996). The nearest site to the specimen cited above, however, is in the Wernecke Mountains about 160 kilometers to the west.

Stellaria media (L.) Vill., Chickweed – YUKON: common invasive garden weed, Burns Road, Whitehorse, *B. Bennett 99-221*, 26 July 1999 (DAO).

This species which is introduced in North America from Eurasia was known to Cody (1996) in the Yukon Territory from only four localities, the nearest of which was adjacent to the Canol Road about 125 kilometers to the east of Whitehorse. It is now a well known weed of gardens in the Whitehorse area.

RANUNCULACEAE

Clematis tangutica (Max.) Korsh., Golden Clematis – YUKON: roadside gravel, across Carcross road from service station side of Highway near Nares Lake, 60°10'N 134°42'W, *B. Bennett 99-543*, 29 Aug. 1999 (B. Bennett Herbarium, photo DAO).

The specimen cited above (which was from the only patch seen) is from about 65 kilometers south of Whitehorse, the only other location known in the Yukon Territory (Cody 1996).

Ranunculus hyperboreus Rottb., Arctic Buttercup – YUKON: in muck border of lagoon near settlement, Pauline Cove, Herschel Island, 69°34'N 138°55'W, *W. J. Cody 36188*, 16 July 1999 (DAO).

This species has not previously been reported from Herschel Island. It is frequent in the southern part of the Yukon Territory north to about latitude 64°30'N adjacent to the Dempster Highway. North of that locality Cody (1996) knew it only from the vicinity of the Bell River and on the Arctic coast in the vicinities of Komakuk Beach and Shingle Point.

Thalictrum alpinum L., Alpine Meadow Rue – YUKON: SW facing slope, small carbonate face 70-100 m above river, 1 km downstream from lower South Bend on east side of river, Snake River, 65°06.5'N 133°07'W, *J. Meikle 99-23*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is about 125 kilometers from a site to the southeast adjacent to the upper Bonnet Plume River and the same distance southwest to a site in the Wernecke Mountains (Cody 1996).

BRASSICACEAE (CRUCIFERAE)

Arabis boivinii G. A. Mulligan (Figure 3) – YUKON: gravel by lake shore, Kathleen Lake adjacent to Haines Highway, 60°35'N 137°18'W, *Cody & Cody 35906*, 8 July 1999 (DAO) (determined by G. A. Mulligan); in gravel in partial shade, Dezadeash Camp Site, 51.3 km S of Haines Junction, 60°24'N 137°02'W, *Cody & Cody 35698*, 30 June 1999 (DAO) (determined by G. A. Mulligan).

This species is new to the flora of the Yukon Territory and should be added to the list of rare species in the Territory (Douglas et al. 1981). A description and key is provided below:

Biennial or short-lived perennial with a simple, compact caudex; stems erect, usually single, simple to few-branched, 30-60 cm high; cauline leaves entire to rarely few-toothed, glabrous to pubescent, sessile, mostly strongly sagittate-clasping stems, narrowly lanceolate, slender petiolate; lower surfaces of caudex leaves with sparse to dense sessile to short-stalked, branched, 3- to 4-parted trichomes mostly 0.35 mm wide; inflorescences semisecund, open; fruiting pedicels arcuate-spreading to arcuate-descending to strongly descending, straight to slightly arcuate, 4.0-6.5 cm long, 1.5-2.0 mm wide; style rudimentary.

This native species is found in widely separated areas in North America: Quebec, Saskatchewan, southwestern

FIGURE 3. *Arabis boivinii* (Drawn by Lee Mennell).

Yukon Territory, Montana and South Dakota.

Arabis boivinii can be separated from *A. divaricarpa* var. *divaricarpa* as follows:

A. Undersurfaces of caudex leaves with unbranched, sessile or nearly sessile, 3-rayed trichomes with rays appressed to leaf surface without numerous prominent branches; inflorescences symmetrical; sliques spreading to ascending *A. divaricarpa* var. *divaricarpa*

A[1]. Undersurfaces of caudex leaves with short-stalked, 3-rayed trichomes with rays elevated above the leaf surfaces with numerous prominent branches; inflorescences semisecund to secund; siliques slightly to strongly descending *A. boivinii*

Arabis drummondii Gray, Drummond's Rockcress – YUKON: stream edge, valley north of Robert Service Mountains [64°25'N 138°11'W], *S. Kojima s.n.*, 28 June 1973 (DAO); valley floor, very wet willow/sedge *Equisetum* basin, Upper Bonnet Plume River Drainage near site #106, 64°25'53.6"N 132°15'11"W, *J. Staniforth 00-032*, 5 July 2000 (DAO) (determined by G. A. Mulligan).

Brooke and Kojima (1985) cited the first specimen above as the northernmost known in the Yukon Territory. It was unfortunately overlooked by Cody (1996) in the writing of the Flora. The second specimen matches the first for the northernmost in the east.

Arabis holboellii Hornem. var. *retrofracta* (Grah.) Rydb., Holboell's Rockcress – YUKON: gravel clearing by road, Dempster Hwy. Km 71, 64°23'N 138°25'W, *Cody & Cody 35728*, 2 July 1999 (DAO).

The specimen cited above is the northernmost yet found in the Yukon Territory (Cody 1996). It is an extension of the known range of about 70 kilometers from near the Klondike Highway-Dempster Highway intersection.

Arabis holboellii Hornem. var. *secunda* (Howell) Jepson, Holboell's Rockcress – YUKON: dry steep slope across Wolf River, Wolf Lake, 60°42.6'N 131°44.08'W, *B. Bennett 99-570A*, 11 Aug. 1999 (DAO) (determined by G. A. Mulligan).

Cody (1996) knew this taxon in the Yukon Territory from only four sites west of longitude 135°W, north to the vicinity of Dawson. The specimen cited above is an extension of the known range in the Territory of about 250 kilometers to the southeast of a site adjacent to the Klondike Highway.

Arabis nuttallii Robins., Nuttall's Rockcress – YUKON: border of salt flats east of Takhini River on north side of Alaska Highway, 60°51'N 135°41'W, *Cody & Cody 35677*, 28 June 1999 (DAO); waste area adjacent to Bedrock Hotel, Mayo, 63°36'N 135°54'W, *Cody & Cody 35776*, 4 July 1999 (DAO); white flats below Elsa, 63°55'N 135°29'W, *Cody & Cody 35785*, 4 July 1999 (DAO) (determined by G. A. Mulligan).

On the basis of two collections in the vicinities of the Tagish Road and Whitehorse, Cody (1994) stated that this species should be added to the list of rare species of the Yukon Territory (Douglas et al. 1981). The specimens cited above extend the known distribution in the Territory westward adjacent to the Alaska Highway and northward about 350 kilometers.

Braya humilis (C. A. Mey.) Robins., Dwarf Braya – YUKON: Jasper Canyon, Snake River, 65°12'N 133°19'W, *J. Meikle 99-024*, 20 July 1999 (Yukon Renewable Resources, photo DAO); silty-sandy soil, broad channelized terrace at confluence of Snake River and tributary stream, 65°42.54'N 133°21.80'W, *J. Meikle 99-025*, 22 July 1999 (Yukon Renewable Resources, photo DAO) (determined by G. A. Mulligan).

This species is scattered throughout much of the Yukon Territory (Cody 1996). The first specimen cited above is about 100 kilometers northwest of a site north of the Upper Bonnet Plume River. The second specimen is from about 140 kilometers southeast of a site in the Richardson Mountains.

Descurainia incisa (Engelm. ex Gray) Britton var. *incisa*, Tansy Mustard – YUKON: disturbed ground adjacent to highway, overlooking Crag Lake, Tagish

Road Km 38, 60°14'N 134°30'W, *Cody & Cody 35888*, 7 July 1999 (DAO) (determined by G. A. Mulligan); open site growing amongst *Dryas* on course gravel, shallow to no soil development on terrace about 3 m above active river course, appears occasionally flooded, Snake River, 65°54.77'N 133°30.50'W, *J. Meikle 99-026B*, July 1999 (Yukon Renewable Resources, photo DAO); soil slide, east bank of stream entering Summit Lake, Richardson Mountains, 67°42'N 136°28'W, *J.G. Packer 1500*, 1 Aug. 1961 (ALTA, photo DAO) (determined by G. A. Mulligan).

This species is new to the flora of the Yukon Territory and should be added to the list of rare species in the Territory (Douglas et al. 1981). A description and key is provided below:

Annual; stems single, usually branched above but sometimes near the base, moderately pubescent to subglabrous; basal leaves pinnately divided, obovate in outline, 5-10 cm long, soon withering; cauline leaves reduced and less divided upward, primary lobes narrowly obovate, these usually deeply dentate to incised; inflorescences elongated, terminating each branch; sepals yellowish to greenish yellow ca. 1.5 mm long; petals spatulate, yellow, ca. 2 mm long; fruiting pedicels 6-12 mm long; siliques terete, narrow, 1 mm or less wide, 6-12 mm long, slightly incurved, glabrous.

This native species is found in western North America from Alberta and British Columbia south to New Mexico and California and is disjunct to the Yukon Territory and central District of Mackenzie. It can be separated from *Descurainea sophia* as follows:

A. Leaves 2- to 3-pinnate; septa of the siliques with 3 distinct nerves; introduced weed *D. sophia*

A[1]. Leaves simply pinnate but pinnae usually dentate or deeply incised; septa nerveless or with 1 distinct nerve; native species but often weedy *D. incisa* var. *incisa*

Descurainia pinnata (Walter) Britt. ssp. *nelsonii* (Rydb.) Detling, (*D. pinnata* (Walter) Britt. ssp. *filipes* sensu Hultén (1968)), Western Tansymustard – YUKON: disturbed ground adjacent to highway, Tagish Road Km 38, 60°15'N 134°30'W, *Cody & Cody 35885*, 7 July 1999 (DAO); gravel in front of buildings, Johnson's Crossing, 60°29'N 133°18'W, *Cody & Cody 35864A*, 7 July 1999 (DAO) (determined by G. A. Mulligan).

Hultén (1968) mapped three localities in the Yukon Territory (Mayo, Kluane Lake and Whitehorse) but voucher specimens were not found in any Canadian herbarium by Douglas et al. (1981) when preparing the rare plant volume. Cody (1996) mapped specimens collected by D. A. Mitchell and J. M. Gillett in 1949 at Whitehorse. The specimens cited above extend the known range in the Territory to the south and east.

Descurainia sophioides (Fischer) O. E. Schulz, Northern Tanseymustard – YUKON: open site growing amongst *Dryas* on coarse gravel, shallow to no soil development on terrace about 3 m above active river course, appears occasionally flooded, Snake River, 65°54.77'N 133°30.50'W, *J. Meikle 99-026A*, July 1999 (Yukon Renewable Resources, photo DAO) (determined by G. A. Mulligan).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 175 kilometers to the east from a site adjacent to the Dempster Highway.

Draba borealis DC., Northern Draba – YUKON: wet tundra, Clarence Lagoon, 69°37'N 140°49'W, *W. J. Cody 26817*, 5 July 1980 (DAO); hummocky lowland near coast, Avadlek Fan, Herschel Island, 69°34.5'N 139°15'W, *W. J. Cody 32280C*, 17 July 1999 (DAO) (determined by G. A. Mulligan).

This species is rare in the Yukon Territory north of latitude 65°02'N adjacent to the Dempster Highway. The specimens cited above are a northern extension of the known range in the Territory of about 500 kilometers. Sites previously mapped by Cody (1996) adjacent to the Peel and Firth rivers have been revised to other species by G. A. Mulligan.

Draba cinerea Adams, Gray-leaved Draba – YUKON: fertile slope adjacent to fox den, approx. 1.5 km E of Pauline Cove, Herschel Island, 69°34'N 138°55'W, *W. J. Cody 36094, 36114B*, 14 July 1999 (DAO) (determined by G. A. Mulligan).

Cody (1996) mapped the northernmost four sites in the Yukon Territory of this species between 68°11'N and 68°34'W. The specimens cited above are a northern extension of the known range in the Territory of about 110 kilometers.

Draba densifolia Nutt., Nuttall's Draba –
The drawing of this species in Cody et al. (2000), *New Records of Vascular Plants in the Yukon Territory II*, Canadian Field-Naturalist 114(3): 433, was by Valerie Fulford, not Lee Mennell.

Draba lonchocarpa Rydb. var. *vestita* O. E. Schulz – YUKON: Kotaneelee Range, 60°14.31'N 124°07.71'W, *B. Bennett 98-598*, 19 June 1998 (DAO) (determined by G. A. Mulligan).

This taxon is new to the flora of the Yukon Territory and is disjunct from coastal British Columbia and the Alaskan Seward Peninsula. It can be distinguished from var. *lonchocarpa* as follows: stem and pedicels frequently pubescent; stems 3 to 15 cm tall, with one or two leaves usually more than 2 mm broad; stellate hairs on lower surfaces of leaves mainly stalked, mainly with eight or less rays; petals white; silicles appressed to stem, glabrous.

Draba nemorosa L. var. *leiocarpa* Lindbl., Wood Whitlow-grass – YUKON: gravel banks of highway, Blackstone River culvert, Dempster Hwy. Km 77.9, 64°50'N 138°20'W, *Cody & Cody 35738*, 2 July 1999 (DAO) (determined by G. A. Mulligan).

This nearly circumpolar species is found only occasionally in the Yukon Territory. The specimen cited above is the northernmost yet found in the Territory, about 30 kilometers north of the northernmost site known to Cody (1996) adjacent to the Dempster Highway.

Draba scotteri G. A. Mulligan, Scotter's Whitlow-grass – YUKON: Kluane National Park: near junction of Kaskawulsh, Dezadeash and Alsek rivers, 60°30'N-60°45'N 137°45'W-138°N, *A. M. Pearson 69-10B*, 30 June 1969 (DAO) (determined by G. A. Mulligan).

Cody (1996) knew only three sites in the Yukon Territory. The specimen cited above is the third known from Kluane National Park.

Draba stenopetala Trautv., Star-flower Draba. – YUKON: alpine scree slope, Mount Skookum, off Annie Lake Road, 60°12'N 135°29'W, *M. Whitley 98-014*, 6 June 1998 (B. Bennett Herbarium, photo DAO); on exposed alpine plateau, Montana Mountain, 60°03'N 134°41'W, *B. Bennett 99-086*, 20 June 1999 (DAO) (determined by G. A. Mulligan).

Douglas et al. (1981) considered this species rare in the Yukon Territory. The specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 140 kilometers to the east from the nearest site in Kluane National Park.

Lepidium densiflorum Schrad. var. *macrocarpum* G. A. Mulligan – YUKON: Klondike River bank opposite Dawson, 64°04'N 139°27'W, *Cody & Ginns 29020*, 6 Aug. 1980 (DAO); disturbed gravel, N side of Pelly River at Ross River, Canol Rd. (N), 61°59'N 132°27'W, *W. J. Cody 26283*, 25 June 1980 (DAO); by building, Ross River Forestry Station, 61°59'N 132°26'W, *Cody & Ginns 28846*, 3 Aug. 1980 (DAO); gravel by regrowth, Pelly Crossing, 62°49'N 136°34'W, *Cody & Cody 35790*, 4 July 1999 (DAO) (determined by G. A. Mulligan).

This variety is new to the flora of the Yukon Territory where it is possibly introduced. Elsewhere in Canada it is found from New Brunswick to British Columbia and south in the United States to Montana, Wyoming and Washington. It can be separated from var. *densifolium* and var. *elongatum* as follows:

A. Siliques puberulent, at least on the margins var. *elongatum*

A¹. Siliques glabrous

B. Siliques averaging 2.5 mm long; pedicels slightly flattened, crowded, more than 9 peduncles per cm var. *densifolium*

B¹. Siliques averaging 3 to 3.5 mm long; pedicels conspicously flattened, less crowded, usually less than 9 pedicels per cm var. *macrocarpum*

Lepidium ramosissimum L., Branched Peppergrass – YUKON: gravel shore of lake, Nunatuk Campground, Frenchman Lake, *Cody & Cody 35805*, 5 July 1999 (DAO) (determined by G. A. Mulligan).

This species which Cody (1996) presumed to be introduced in the Yukon Territory was known to him from only three localities. The specimen cited above is intermediate between two sites adjacent to the Klondike Highway.

Parrya arctica R.Br. – YUKON: slope overlooking bay, Pauline Cove Settlement, Herschel Island, 69°34'N 138°55'W, *W. J. Cody 36030*, 13 July 1999 (DAO) (determined by G. A. Mulligan).

The only other collection of this species in the Yukon Territory was also from Herschel Island where it was found by P.F. Cooper at top of cliffs just east of Boot Eating Creek on 9 May 1979. It is endemic to the Canadian Arctic Archipelago (Cody 1994) and should be added to the list of Rare Plants in the Yukon Territory (Douglas et al. 1981).

Rorippa palustris (L.) Besser, Marsh Yellow Cress – YUKON: marsh, Taber Lake, 66°58'42.36"N 134°46'55.51"W, *G. Brunner 2-99*, 23 June 1999 (Yukon Renewable Resources, photo DAO) (determined by G. A. Mulligan).

The specimen cited above from the Peel River Valley is an extension of the known range in the Yukon Territory of about 175 kilometers to the northeast from a site adjacent to the Dempster Highway and 90 kilometers to the southeast from a site adjacent to the Rat River (Cody 1996).

Thlaspi arvense L., Field Pennycress – YUKON: stony bank by house, Keno, 63°55'N 135°18'W, *Cody & Cody 35783*, 4 July 1999 (DAO).

This species is an occasional introduction as far north in the Yukon Territory as Dawson. The specimen cited above from Keno is about 150 kilometers east of a site at the south end of the Dempster Highway and 150 kilometers northeast of a site adjacent to the Klondike Highway (Cody 1996).

CRASSULACEAE

Rhodiola rosea L. ssp. *integrifolia* (Raf.) Hara, Roseroot – YUKON: just north of Albert Creek near the Little Rancheria River, ca 60°10'N 129°30'W, *B. Bennett 97-53*, July 1995 (DAO).

The specimen cited above is an extension of the known range in the Territory of about 150 kilometers south of a site just north of the Robert Campbell Highway known to Cody (1996).

SAXIFRAGACEAE

Boykinia richardsonii (Hook.) A. Gray, Richardson's Boykinia – YUKON: on sub peak and adjacent valley to Mt. McDonald, Snake River, 64°43'N 132°44'W, *J. Meikle 99-027*, 17 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is the easternmost yet found in the Yukon Territory (Cody 1996) and is near the southern limit in the Territory.

Saxifraga adscendens L. ssp. *oregonensis* (Raf.) Breitung, Wedge-leaved Saxifrage – YUKON: steep rocky slope above stream, Ogilvie Mountains, Patrol Range, east of Chandindu River 64°45'N 139°06'W, *W. J. Cody 36603B*, 20-22 July 1999 (DAO).

This cordilleran taxon is scattered in southern Yukon Territory and then disjunct to a site adjacent to the Canol Road near the District of Mackenzie border and two sites north of latitude 64°N (Cody 1996). The specimen cited above, which is the northernmost yet found in the Territory, is from about 55 kilometers northwest of a site adjacent to the Dempster Highway.

Saxifraga aizoides L., Yellow Mountain Saxifrage – YUKON: Jasper Canyon, Snake River, 65°24'N 133°24'W, *J. Meikle 99-028*, 20 July 1999 (Yukon Renewable Resources, photo DAO); undulating spruce/shrub/lowshrub/forb/moss, Upper Bonnet Plume River Drainage Site #105, *J. Staniforth 00-012*, 5 July 2000 (DAO).

Douglas et al. (1981) considered this species rare in the Yukon Territory. The specimens cited above were found about 75 kilometers northeast of a site between the Wind

and Bonnet Plume rivers and about 65 kilometers east of a site adjacent to the Upper Wind River.

Saxifraga bronchialis L. ssp. *funstonii* (Small) Hultén, Spotted Saxifrage – YUKON: Jasper Canyon growing in moist crag in limestone, Snake River, 65°24'N 133°24'W, *J. Meikle 99-029*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is the easternmost of this species yet found in the Yukon Territory (Cody 1996). The nearest collections are from the Richardson Mountains about 160 kilometers to the northwest and adjacent to latitude 64°N, 275 kilometers to the southwest.

ROSACEAE

Geum aleppicum Jacq. ssp. *strictum* (Ait.) Clausen, Yellow Avens – YUKON: Galkeno wetland, Keno City, 63°55.1'N 135°20.3'W, *S. Withers 500*, 10 Aug. 1999 (B. Bennett Herbarium, photo DAO).

The specimen cited above is an extension of the known range of this species in the Yukon Territory (Cody 1996) northward about 230 kilometers from a site adjacent to the Klondike Highway. This species was considered rare in the Territory by Douglas et al. (1981).

Potentilla norvegica L., Norwegian Cinquefoil – YUKON: marsh, Taber Lake, 66°58'42.36"N 134°46'55.51"W, *G. Brunner 3-99*, 23 June 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range of about 175 kilometers northeast of a site adjacent to the Dempster Highway (Cody 1996). To the northwest there is a site just south of latitude 68°N, a distance of about 225 kilometers.

Potentilla rubricaulis Lehmann – YUKON: steep dry exposed cliff face, Upper Wolf River, 60°41.8'N 131°47.22'W, *B. Bennett 99-442*, 12 Aug. 1999 (DAO).

This species was uncommon in the Yukon Territory west of longitude 133°W (Cody 1996). The specimen cited above is an extension of the known range in the Territory of about 150 kilometers to the southeast of a site mapped adjacent to the Canol Road.

Rubus chamaemorus L., Cloudberry – YUKON: Jasper Canyon, Snake River, 65°24'N 133°24'W, *J. Meikle 99-031*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

This is a widespread species in the Yukon Territory (Cody 1996). The nearest collections to the specimen cited above are from south of the Peel River about 140 kilometers to the northwest and adjacent to the Bonnet Plume River about 150 kilometers to the southeast.

Rubus pubescens Raf., Dwarf Raspberry – YUKON: open tall *Abies*/ feathermoss forest, approx. 5 km W of Rancheria, 60°06'25"N 130°41'05"W, *C. Zoladeski 98-25-4*, 1 Aug. 1998 (DAO).

This is a rare species in the Yukon Territory (Douglas et al. 1981). Cody et al. (1998) cited a number of new sites in the southeastern part of the Territory. The specimen cited above is an extension of the known range in the Territory of about 120 kilometers west from south of Upper Liard Village that is west of Watson Lake.

Sorbaria sorbifolia A. Braun, False Spiraea (Figure 4) – YUKON: garden escape, Dawson, *S.M. Landhausser s.n.*, 30 July 1992 (DAO); found growing and spreading in an empty lot near Robert Service cabin, Dawson City, 64°03.23'N 139°25.8'W, *B. Bennett 99-253*, 1 Aug. 1999 (B. Bennett Herbarium, photo DAO).

This shrub is introduced from eastern Asia. In Canada it has been found escaped from cultivation from Newfoundland to Alberta and is now new to the flora of the Yukon Territory. The genus *Sorbaria* can be distinguished from *Spiraea* as follows:

A. Leaves simple, stipules absent or caducous	*Spiraea*
A[1]. Leaves compound, stipulate	*Sorbaria*

FABACEAE (LEGUMINOSAE)

Astragalus adsurgens Pall. ssp. *robustior* (Hook.) Welsh, Standing Milk-vetch – YUKON: gravel of roadstop, 19 km from Stewart Crossing on Silver Trail Hwy., *Cody & Cody 35764*, 3 July 1999 (DAO).

This is a rare taxon in the Yukon Territory (Cody 1996). The specimen cited above is an extension of the known range of about 220 kilometers to the northwest from a site adjacent to Faro on the Campbell Highway.

Astragalus cicer L., Chick-pea Milk-vetch – YUKON: roadside photograph, Haines Highway near Klukshu, ±60°17'30"N 137°W, *B. Bennett s.n.*, Oct. 1995 (DAO).

The only other record of this introduced species in the Yukon Territory is from a roadside adjacent to the La Biche River in the extreme southeast (Cody et al. 1998).

FIGURE 4. *Sorbaria sorbifolia* (Drawn by Lee Menell).

Caragana arborescens Lam., Common Caragana – YUKON: ornamental shrub, commonly escaping cultivation, Dawson, 64°03.23'N 139°25.8'W, *B. Bennett 99-251*, 1 Aug. 1999; commonly escaping shrub, Whitehorse, 60°42.84'N 135°02.95'W, *B. Bennett 99-220*, 26 July 1999 (B. Bennett Herbarium, photo DAO).

Cody et al. (2000) reported the finding of this escaping shrub in the Dawson area in 1949. The specimens cited above suggest its continued escaping in Dawson and also in Whitehorse.

Medicago falcata L., Yellow Lucerne – YUKON: roadside, north Klondike Hwy., Km 478, 63°02.76'N 136°25.72'W, *B. Bennett 99-294*, 31 July 1999 (DAO); Faro-Campbell Hwy., 62°14'N 133°20'W, *Cody & Cody 35810a*, 5 July 1999 (DAO); parking area adjacent to highway, Haines Hwy. Km 202.3, 60°30'N 137°03'W, *Cody & Cody 35974*, 9 July 1999 (DAO).

Cody (1996) recorded only four locations where this introduced plant had been found. An additional three locations are cited above. This is now widespread in southwestern Yukon.

Medicago sativa L., Alfalfa – YUKON: numerous collections by B. Bennett of this species were made from adjacent to the Klondike, Campbell and Alaska highways between longitudes 134°W and 138°34'W during the summer of 1999 where presumably they were the result of roadside seeding. Prior to that it was only known from the vicinity of Whitehorse (Cody 1996) and in the La Biche area (Cody et al. 1998).

Melilotus alba Desv., White Sweet-clover – YUKON: gravel bank by Klondike Hwy., 61°32'N 135°57'W, *Cody & Cody 35713*, 30 June 1999 (DAO); found on Front Street, Dawson City, 64°03.23'N 139°25.8'W, *B. Bennett 99-252*, 1 Aug. 1999 (DAO); small patch, Dempster Hwy. Km 22, 64°06.93'N 138°32.42'W, *B. Bennett 99-272*, 1 Aug. 1999 (DAO).

Cody (1996) knew this introduced species as far north as about latitude 62°20'N adjacent to the Klondike Highway and then disjunct to the vicinity of Mayo. The specimens cited above extend the known distribution in the Territory north to Dawson and the southern Dempster Highway.

Melilotus officinalis (L.) Lam., Yellow Sweet-clover – YUKON: roadside, North Klondike Hwy. Km 478, North of Pelly Crossing, 63°02.76'N 136°25.72'W, *B. Bennett 99-293*, 31 July 1999 (DAO); roadside, North Klondike Hwy. Km 666, Klondike Hill, 63°55.33'N 138°33.31'W, *B. Bennett 99-255*, 1 Aug. 1999 (DAO); Guggieville, Dawson City, 64°02.49'N 139°23.34'W, *B. Bennett 99-254*, 1 Aug. 1999 (DAO).

Cody (1996) knew this introduced species as far north on the Klondike Highway as the vicinity of Carmacks and then disjunct to the vicinity of Mayo. The specimens cited above extend the known distribution in the Yukon Territory northwest along the Klondike Highway to Dawson.

Oxytropis campestris (L.) DC. ssp. *jordalii* (A.E. Porsild) Hultén, Late Yellow Locoweed – YUKON: moist pockets in talus, Kotaneelee Range, 60°14'31"N 124°07'19"W, *B. Bennett 98-607*, 19 June 1998 (DAO).

Cody (1996) knew this species in the Yukon Territory to be frequent north of latitude 64°N and rare in the south in the Carcross area. The specimen cited above is about 575 kilometers east of the Carcross region and 650 kilometers southeast of the nearest northern site. It is, however, known in the southern Mackenzie Mountains to the east.

Oxytropis deflexa (Pall.) DC. ssp. *foliolosa* (Hook.) Cody, Pendant-pod Locoweed – YUKON: growing in sandy soil on broad semi-active floodplain, Snake River, 65°42.54'N 133°21.80'W, *J. Meikle 99-034*, 22 July 1999.

This species is widespread in the Yukon Territory (Cody 1996). The nearest site to the specimen cited above is about 140 kilometers to the northwest.

Oxytropis deflexa (Pall.) DC. ssp. *sericea* (T.& G.) Cody, Pendant-pod Locoweed – YUKON: in roadside gravel on edge of river, Ogilvie Mountains near Ogilvie River, *B. Bennett 99-032*, 15 June 1999 (DAO).

Cody (1996) knew this taxon in the Yukon Territory only from the vicinity of Dawson and south of latitude 64°N. The specimen cited above is an extension of about 150 kilometers north of the Dawson area adjacent to the Dempster Highway.

Oxytropis scammaniana Hultén, Scamman's Locoweed – YUKON: lower carboniferous gray shale, head of Kandik River, 65°41'N 140°28'W, *O. Hughes s.n.*, 18 Aug. 1962 (DAO).

Cody (1996) knew this species in the Yukon Territory only as far north as the southwestern Ogilvie Mountains. The specimen cited above is an extension of the known range in the Territory of about 150 kilometers to the northwest.

Vicia cracca L., Tufted Vetch – YUKON: roadside, downtown 6th and Hansen, Whitehorse, 60°42.84'N 132°02.95'W, *B. Bennett 99-112*, 14 July 1999 (DAO).

Cody (1996) knew this introduced species in the Yukon Territory only from a collection in the vicinity of Dawson. Cody et al. (2000) reported a second collection from Wye Lake south of Watson Lake.

APIACEAE (UMBELLIFERAE)

Angelica lucida L., Seacoast Angelica – YUKON: along creek, Haines Hwy. Km 145.8, ½ km N of British Columbia border, 60°05'N 136°51'W, *Cody & Cody 35960*, 9 July 1999 (DAO); low moist area below road, Haines Hwy. Km 158 south of Million Dollar Falls, 60°06.5'N 136°56'W, *Cody & Cody 35957*, 9 July 1999 (DAO); many small patches in stony soil at back of beach in partial shade of *Salix* and *Populus*, about 12 m back from lake shore and adjacent to gravel roadside in partial shade of *Populus balsamifera*, Dezadeash Camp Site, 60°24'N 137°02'W, *Cody & Cody 35692*, 29 June

1999 (DAO); in open area adjacent to *Populus tremuloides*, Haines Hwy. north of Dezadeash Lake, 60°34'N 137°08'W, *Cody & Cody 35975*, 9 July 1999 (DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory only from southeastern Kluane National Park and Macmillan Pass. Cody (1994) and Cody et al. (1998, 2000) added three additional locations, including the extreme southeast of the Territory. As can be seen from the collections cited above, this species is quite frequent in the terrain adjacent to the Haines Highway north of the British Columbia border to latitude 60°34'N.

Cicuta virosa L., European Water-Hemlock – YUKON: bog, Taber Lake, 66°58'30.19"N 134°45'50.66"W, *G. Brunner 7-99*, 25 June 1999 (Yukon Renewable Resources, photo DAO); marsh, Vittrewka Lake, 66°49'8.68"N 135°29'10.32"W, *G. Brunner 32-99*, 29 June 1999 (Yukon Renewable Resources, photo DAO); wet creek bank with willow, Mica Creek, 62°48.1'N 136°34.2'W, *S. Withers SW00-052*, 14 July 2000 (DAO).

Cody (1996) knew this species from scattered sites in the Yukon Territory north to Mayo and Dawson and then disjunct to the western Porcupine River area. The first two specimens cited above from the Peel River wetlands are from sites about 375 kilometers north of Dawson and Mayo and 200 kilometers southeast of the Porcupine River area. The third specimen is from a site about 100 kilometers southwest of the vicinity of Mayo.

PYROLACEAE

Pyrola minor L., Lesser Wintergreen – YUKON: well drained alluvial soil on bench 3 m above river, Snake River, 65°01'N 133°07'W, *J. Meikle 99-039*, 19 July 1999 (Yukon Renewable Resources, photo DAO); steep slope, Ogilvie Mountains, Patrol Range, east of Chandindu River, 64°45'N 139°06'W, *W. J. Cody 36582*, 20-22 July 1999 (DAO); Vittrewka Lake, 66°49'28.26"N 135°29'45.19"W, *G. Brunner 18-99*, 27 June 1999 (Yukon Renewable Resources, photo DAO).

Cody (1996) knew this species in the Yukon Territory only as far north as about latitude 64°30'N from sites in the Wernecke Mountains, adjacent to the Dempster Highway, and west of Dawson adjacent to the Top of the World Highway. The specimens cited above are extensions of the known range about 70 kilometers northwest of the Dempster Highway site, 115 kilometers northeast of the Wernecke Mountains site and about 275 kilometers north of the Wernecke Mountains site.

ERICACEAE

Cassiope tetragona (L.) D. Don ssp. *saximontana* (Small) A. E. Porsild, Four-angled Mountain-heather – YUKON: hummocky terrain, White Hat Hills, Tombstone Range, Ogilvie Mountains, 64°45.20'N 138°29.113'W, *W. J. Cody 36431*, 20-22 July 1999 (DAO); open *Picea glauca* wooded slope, 10 miles north of Chapman Lake, Ogilvie Mountains, 64°58'N 138°2.5'W, *Cody & Ginns 33972*, 8 July 1984 (DAO).

Cody (1996) mapped two sites north of latitude 64°N in the Yukon Territory: west of Dawson adjacent to the 60 Mile Road (Top of the World Highway) and east of the Dempster Highway in the Wernecke Mountains. Unfortunately, the second site was incorrectly mapped and should have been the second locality cited above. The two locations cited above extend the known range in the Territory north of a site near the junction of the Klondike and Dempster highways about 120 kilometers.

Kalmia polifolia Wang., Bog-laurel – YUKON: undulating slope, "Tree Arc" west of Chapman Lake, Tombstone Range, 64°51'N 138°30'W, *W. J. Cody 36787*, 20–22 July 1999 (DAO).

Cody (1996) unfortunately did not map a location adjacent to the Dempster Highway cited by Brooke and Kojima (1985). The specimen cited above is an extension of the known range in the Ogilvie area of about 80 kilometers to the north. Cody et al. (2000) did, however, report a site north of latitude 67°N in the Porcupine River area.

Phyllodoce × *intermedia* (Hook.) Rydb. – YUKON: in moist woodland, Mile 140 Haines Road (near Kathleen Lake), *J. Y. Tsukamoto s.n.*, July 1961 (DAO).

The specimen cited above was unfortunately missed during the preparation of the Flora of the Yukon Territory (Cody 1996). This hybrid between Phyllodoce empetriformis and P. glanduliflora can be distinguished by its somewhat glandular calyx and the corolla pinkish and glabrous to slightly glandular.

PRIMULACEAE

Androsace septentrionalis L. – Fairy-candelabra – YUKON: in gravel on road that goes down to creek, Dempster Hwy. near Km 100, 64°49.144'N 138°21.023'W, *B. Bennett 99-006*, 15 June 1999 (DAO).

This species was known to Cody (1996) mostly south of latitude 64°N and then disjunct to the Porcupine River. The specimen cited above is an extension of the known range northward along the Dempster Highway of about 95 kilometers.

LAMIACEAE (LABIATAE)

Galeopsis tetrahit L. ssp. *bifida* (Boenn.) Fries, Hempnettle – YUKON: growing in garden, Granger neighbourhood, City of Whitehorse, 60°42'N 135°05'W, *J. McIntyre s.n.*, 27 Sept. 1999 (DAO).

This is the third locality in the Yukon Territory where this species that is introduced from Eurasia has been found (Cody 1996; Cody et al. 1998).

Mentha arvensis L., Field Mint – YUKON: bog, Taber Lake, 66°59'20.87"N 134°44'29.67"W, *G. Brunner 4-99*, 24 June 1999 (Yukon Renewable Resources, photo DAO).

Cody (1996) knew this species in the Yukon Territory north almost to latitude 64°N. The specimen cited above is an extension of the known range in the Territory of about 360 kilometers from a site north of Mayo.

SCROPHULARIACEAE

Castilleja caudata (Pennell) Rebr. – YUKON: coarse gravel in thin to little soil on high energy riverbank, Snake River, 65°06'N 133°05'W, *J.*

Meikle 99-042, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 175 kilometers to the southeast from a site in the southern Richardson Mountains.

Castilleja miniata Dougl. ex Hook., Scarlet or Common Red Paintbrush – YUKON: brush, gravelly roadbank, Top of the World Hwy., 29.9 mi W of W. Dawson ferry docking, *M. Egger 432*, 4 July 1991 (WTU, photo DAO).

Scotter and Cody (1979) reported the first record of this rare species in the Yukon Territory from the vicinity of Larsen Creek in the extreme southeast. C. E. Kennedy collected another specimen nearby adjacent to the Coal River Springs in 1983 (DAO) and Douglas et al. (1981) mapped a collection from the vicinity of Atlin Lake about 750 kilometers to the west. The specimen cited above was reported by Egger (1992) who suggested that this range extension of over 400 kilometers to the north was probably the result of seed being carried on an automobile tire from the south. The specimen cited above was unfortunately missed during the preparation of the Flora of the Yukon Territory (Cody 1996).

Castilleja pallida (L.) Spreng. ssp. *candata* Pennell – YUKON: moist pockets in talus, Kotaneelee Range, 60°14'31"N 124°07'19"W, *B. Bennett 98-567*, 19 June 1998 (B. Bennett Herbarium, photo DAO) (determined by M. Egger).

This species is widespread in the Yukon Territory west of longitude 134°W (Cody 1996). The specimen cited above is an extension of the known range of about 575 kilometers to the extreme southeast.

Castilleja raupii Pennell, Raup's Paintbrush – YUKON: in sandy soil over gravel on riverbank on braided channel, Snake River, 64°45.57'N 132°35.81'W, *J. Meikle 99-044*, 18 July 1999 (Yukon Renewable Resources, photo DAO); riverbar, Wind River, 65°05.97'N 135°05.23'W, *B. Bennett 00-462*, 4 July 2000 (B. Bennett Herbarium, photo DAO); open well washed riverbar, Peel River, 65°55.97'N 135°02.99'W, *B. Bennett 00-383*, 9 July 2000 (B. Bennett Herbarium, photo DAO); riverbar, Peel River Camp #8, 65°56.03'N 134°58.84'W, *B. Bennett 00-773*, 9 July 2000 (B. Bennett Herbarium, photo DAO).

The specimens cited above are an extension of the known range in the Yukon Territory (Cody 1996) of about 200 kilometers southeast of a site in the southern Richardson Mountains.

Limosella aquatica L., Water Mudwort – YUKON: wet ditch with *Callitriche verna*, La Biche Airstrip, 60°07'42"N 124°02'21"W, *B. Bennett 98-579*, 14 June 1998 (DAO).

Douglas et al. (1981) knew this rare species in the Yukon Territory only from the vicinity of Mount Sheldon adjacent to the Canol Road. Cody (1994), Cody et al. (1998, 2000) added additional sites at the Nisutlin River Delta, Liard River south of Watson Lake and the Old Crow Flats. The specimen cited above is an extension of the known range of about 240 kilometers east of the Liard River location.

Pedicularis macrodonta Richards., Small-flowered Lousewort – YUKON: fen, Turner Lake, 66°11'06.09"N 134°16'45.14"W, *G. Brunner 49-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO).

This species is listed as rare in Douglas et al. (1981). Cody (1996) knew it only in the Yukon Territory from two localities in the extreme south. The specimen cited above from the Peel River wetland area is an extension of the known range northward about 700 kilometers.

Pedicularis verticillata L., Whorled Lousewort – YUKON: open white spruce forest on terrace elevated enough to avoid seasonal flooding, Snake River, *J. Meikle 99-046*, 65°01'N 133°07'W, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 200 kilometers east of a site in the mountains adjacent to the Hart River.

LENTIBULARIACEAE

Pinguicula vulgaris L. ssp. *vulgaris*, Common Butterwort – YUKON: growing on wet moss on limestone, Jasper Canyon, Snake River, 65°24'N 133°24'W, *J. Meikle 99-041*, 20 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 135 kilometers north of a site near the headwaters of the Wind River.

Utricularia intermedia Hayne, Flat-leaved Bladderwort – YUKON: bog, Turner Lake, 66°11'06.09"N 134°16'45.14"W, *G. Brunner 46-99*, 2 July 1999 (Yukon Renewable Resources, photo DAO).

Douglas et al. (1981) considered this circumpolar species to be rare in the Yukon Territory. Cody (1996) knew scattered collections north to about latitude 64°N and then disjunct to the Porcupine River valley. The specimen from the Peel River wetlands area cited above is about 250 kilometers north of a site just north of Mayo and 280 kilometers southeast of the Porcupine River area.

Utricularia vulgaris L. ssp. *macrorhiza* (LeConte) Clausen, Greater Bladderwort – YUKON: marsh, Taber Lake, 68°59'40.05"N 134°47'22.90"W, *G. Brunner 6-99*, 24 June 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above from the Peel River wetlands area is from a site about 115 kilometers east of a site in the Richardson Mountains reported by Cody et al. (2000).

ADOXACEAE

Adoxa moschatellina L., Moschatel

Cody (1996) stated that this circumpolar species was monotypic in the genus *Adoxa* and that *Adoxa* was the only genus of the family Adoxaceae. It has recently been brought to our attention (Hong Qian in correspondence 1999) that Liang and Wu (1995) state that the family Adoxaceae is now divided into 3 genera and four species, all of which occur in China: *A. moschatellina* L., *A. orientalis* Nepomn., *Sinadoxa corydalifolia* C. Y. Wu, Z. L. Wu and R. F. Huang and *Tetradoxa omeiensis* (Hara) C. Y. Wu.

ASTERACEAE (COMPOSITAE)

Antennaria densifolia A. E. Porsild, Dense-leaved Pussytoes – YUKON: Jasper Canyon, Snake River, 65°24'N 133°24'W, *J. Meikle 99-048*, 20 July 1999 (Yukon Renewable Resources, photo DAO); Wind River, 64°40.39'N, 64°48.46'N, 64°51.83'N, 65°06.83'N, 65°22.89'N, 65°36.03'N, *B. Bennett 00-754, 00-316, 00-821, 00-158, 00-191, 00-170, 00-277* (DAO).

The specimens cited above are the easternmost record of this endemic species in the Yukon Territory (Cody 1996). The nearest collections are just north of latitude 66°N about 125 kilometers to the northwest, and adjacent to the Hart River about 175 kilometers to the west. This species is, however, known in the Mackenzie Mountains to the east (Porsild and Cody 1980).

Antennaria pulcherrima (Hook.) Greene, Showy Pussytoes – YUKON: riverbar, Wind River Camp #1, 64°40.39'N 134°35.96'W, *B. Bennett 00-352*, 2 July 2000 (DAO); Canyon, Snake River, 65°12.32'N 133°19.70'W, *J. Meikle 99-049*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimens cited above are the northernmost yet recorded in the Yukon Territory (Cody 1996). They are extensions of the known range in the Territory of about 100 kilometers to the north and northwest from a site adjacent to the upper Bonnet Plume River.

Artemisia michauxiana Bess. in Hook., Michaux's Mugwort – YUKON: sand beach, Carcross, 60°10'N 134°42'W, *Cody & Cody 35890*, 7 July 1999 (DAO).

This species, which was considered rare in the Yukon Territory by Douglas et al. (1981) was previously known in the Territory only from the vicinity of Little Atlin Lake about 50 kilometers to the northeast of the specimen cited above.

Artemisia tilesii Ledeb. sl., Aleutian Mugwort – YUKON: collected amongst *Dryas* – widely braided channel, seasonally flooded, Snake River, 65°24.83'N 133°24.60'W, *J. Meikle 99-050*, 21 July 1999 (Yukon Renewable Resources, photo DAO).

This is a widespread species in the Yukon Territory (Cody 1996). The specimen cited above, however, is from a site about 140 kilometers northwest of the nearest location adjacent to the upper Bonnet Plume River.

Centaurea cyanus L., Bachelor's-button (Figure 5) – YUKON: along railway tracks at Yukon River, Whitehorse, *S. M. Landhaüsser s.n.*, 1992 (DAO); Dawson Dike along Yukon River, *S.M. Landhaüsser s.n.*, 1992 (DAO).

Not previously reported as occurring in the Yukon Territory; Douglas et al. (1989) stated that this species, which is introduced from the Mediterranean region, is a frequent garden escape along roadsides in southern British Columbia but in our experience it is not persistent in the Yukon Territory.

Crepis elegans Hook., Elegant Hawksbeard – YUKON: growing in sandy soil on broad semi-active flood plain, Snake River, 65°42.51'N 133°21.80'W, *J. Meikle 99-052*, 22 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 75 kilometers southeast of a site adjacent to the Peel River.

Crepis tectorum L., Annual Hawk's-beard – YUKON: built up river bar, Mayo, 63°36'N 135°54'W, *Cody & Cody 35775*, 3 July 1999 (DAO).

The nearest site of this introduced species known to Cody (1996) is adjacent to the Klondike Highway in the vicinity of Minto, about 100 kilometers to the southwest. To the northwest it has also been found in the vicinity of Dawson.

Erigeron acris L. ssp. *politus* (Fries) Schinz & Keller, Bitter Fleabane – YUKON: Snake River, 65°42.54'N 133°21.80'W, *J. Meikle 99-053*, 22 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 150 kilometers southeast from a site in the southern Richardson Mountains.

Erigeron elatus (Hook.) Greene – YUKON: McDonald Camp on gravelly soil in semi-active floodplain of river, Snake River, 64°45.57'N 132°35.81'W, *J. Meikle 99-054*, 18 July 1999 (Yukon Renewable Resources, photo DAO); in gravels in open riverbar, Wind River, 65°12.49'N 135°13.17'W, *B. Bennett 00-459*, 5 July 2000 (B. Bennett Herbarium, photo DAO); open riverbar in gravels, Illytd Creek confluence with Wind River, 65°30.07'N 135°22.88'W, *B. Bennett 00-105*, 6 July 2000 (B. Bennett Herbarium, photo DAO).

The specimens cited above are extensions of the known range in the Yukon Territory (Cody 1996) of about 130 kilometers east and north from a site in the Wernecke Mountains.

Petasites frigidus (L.) Fries ssp. *frigidus*, Sweet Coltsfoot – YUKON: in open White Spruce forest on terrace 3 m above river, Snake River, 65°01'N 133°07'W, *J. Meikle 99-055*, 19 July 1999 (Yukon Renewable Resources, photo DAO).

The specimen cited above is an extension of the known range in the Yukon Territory (Cody 1996) of about 100 kilometers northwest of a site adjacent to the upper Bonnet Plume River.

Senecio hyperborealis Greenm., Boreal Groundsel – YUKON: open dolomite delta, Wind River, 64°48.46'N 134°41.34'W, *B. Bennett 00-225, 00-294, 00-320*, 3 July 2000 (DAO); in talus at base of cliff, Wind River, 65°12.49'N 135°13.17'W, *B. Bennett 00-368*, 5 July 2000 (DAO); loose talus at base of steep active shale scree slope, junction of Wind and Peel rivers Camp #7, 65°50.48'N 135°18.25'W, *B. Bennett 00-785, 00-809*, 8 July 2000 (DAO); river bank, fine silty soil, below active scree slope, on seasonal floodplain, Snake River, 65°56'N 133°17'W, *J. Meikle 99-057*, 22 July 1999

FIGURE 5. *Centaurea cyanus* (Drawn by Iljvars Steins).

(Yukon Renewable Resources, photo DAO); undulating dry hummocky tundra alpine slope, Upper Bonnet Plume River Drainage Site #116, 64°24'28.7"N 132°07'54"W, *J. Staniforth 00-082*, 7 July 2000 (DAO).

This species, endemic to arctic and subarctic northwestern North America was not included in the rare plants of the Yukon Territory (Douglas et al. 1981) because it was too widespread. The specimens cited above are an extension of the known range in the Territory (Cody 1996) of about 100 kilometers east and 225 kilometers southeast of sites in the southern Richardson Mountains.

Senecio lugens Richards., Black-tipped Groundsel – YUKON: in hummocky *Picea/Salix* forest near river, Wind River, 64°34.19'N 134°25.77'W, *B. Bennett 00-347*, 2 July 2000 (DAO); in White Spruce forest on moss, Snake River, 64°57.16'N 133°00.21'W, *J. Meikle 99-058*, 19 July 1999 (Yukon Renewable Resources, photo DAO); undulating upper slope, Upper Bonnet Plume River Drainage Site #125, 64°32'45"N 132°50'48"W, *J. Staniforth 00-098*, 8 July 2000 (DAO).

This is a common species throughout much of the Yukon Territory (Cody 1996). The specimens cited above are an extension of the known range in the Territory of about 150 kilometers northeast of the vicinity of Mayo.

Sonchus arvensis L. ssp. *uliginosus* (Bieb.) Nyman, Perennial Sow-thistle – YUKON: roadside overlooking Teslin Lake, near Brooks Brook, 60°25.607'N 133°11.942'W, *B. Bennett 99-538*, 16 Aug. 1999 (DAO).

Cody (1996) knew this species, introduced from Europe, from only four localities in the southern part of the Yukon Territory. Cody et al. (1998, 2000) added new sites from Whitehorse and the La Biche areas. The specimen cited above is from about 125 kilometers southeast of Whitehorse.

Taraxacum carneocoloratum A. Nels. – YUKON: on ridge top, North Fork Pass, Ogilvie Mountains, Dempster Highway, 64°36'N 138°20'W, *C. Parker 1191*, 8 July 1984 (ALA, photo DAO).

This species was described from specimens collected in the McKinley park area between Fairbanks and Anchorage in Alaska and was reported as new to the Flora of the Yukon Territory by A. E. Porsild (1975) on the basis of specimens collected by his brother R. T. Porsild adjacent to the Dempster Highway, but was unfortunately overlooked by Cody (1996). It should be added to the list of rare plants in the Territory (Douglas et al. 1981). The following description is from Hultén (1968): Low-growing; leaves oblong-lanceolate, with 3-5 pairs of triangular, somewhat acute lobes; terminal lobe comparatively large, ovate-triangular, blunt; petioles pale at base; heads often wooly at base; outer bracts broadly ovate, purplish, scarious-margined, indistinctly corniculate; ligules up to 18 mm long, about 1 mm broad, pink to flesh-coloured; achenes spinulose-muricate at tip, with beak about as long as achene.

Taraxacum officinale Weber ex Wiggers, Common Dandelion – YUKON: common along Alaska Highway right-of-way up to Haines Junction and north to Kluane Lake, south to Dezadeash Campground, 60°24'N 137°02'W, *Cody & Cody 35690*, 29 June 1999 (DAO); Tombstone Campground, 64°23'N 138°25'W, *Cody & Cody 35729*, 2 July 1999 (DAO); gravel roadside, Dempster Hwy. Km 74, 63°25'N 138°20'W, *Cody & Cody 35742*, 2 July 1999 (DAO);

roadside gravel, Dempster Hwy. Km. 109, 64°48.592'N 138°21.438'W, *B. Bennett 99-078*, 16 June 1999 (B. Bennett Herbarium, photo DAO).

This invasive weed has expanded greatly since I travelled the Haines, Alaska and Klondike highways in the early 1980's. It now occupies extensive areas along the roadsides in the southwest of the Territory and appears to be spreading northward up the Dempster Highway.

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Observations of Change in the Cover of Polargrass, *Arctagrostis latifolia*, and Arctic Lupine, *Lupinus arcticus*, in Upland Tundra on Herschel Island, Yukon Territory

C. E. Kennedy[1] , C. A. S. Smith[2], and D. A. Cooley[3]

[1]Fish and Wildlife Branch, Yukon Department of Renewable Resources, Box 2703, Whitehorse, Yukon Territory Y1A 2C6 Canada

[2]Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada, 4200 Hwy 97, Summerland, British Columbia V0H 1Z0 Canada

[3]Fish and Wildlife Branch, Yukon Department of Renewable Resources, Box 600, Dawson City, Yukon Territory Y0B 1G0 Canada

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Herschel Island is located in the southern Beaufort Sea off the northern coast of the Yukon Territory and has acted as an excellent observatory of environmental change in the Canadian western Arctic. Between 1986 and 1999 the percentage cover of Polargrass (*Arctagrostis latifolia* (R.Br.) Griseb.) was observed to increase from 1% to > 5% in a dominant upland tundra vegetation type on Herschel Island. For example, the Arctic Willow/Dryas-Vetch type which occurs extensively on undulating portions of the island's upland and is associated with periglacial processes leading to patterned ground formation, has undergone a notable physiognomic change. Initially characterized by low shrubs and forbs, it is now characterized by grass. Similarly, the cover value of Arctic Lupine *(Lupinus arcticus* S. Wats.) increased markedly on many of the sites inventoried within this same vegetation type. Temperature records from Inuvik in the nearby Mackenzie Delta, suggest that the last 15 years have been warmer and somewhat drier than the 30 year normal in the region. Much of this increased cover of *Arctagrostis latifolia* and *Lupinus arcticus* is occurring on the bare patches of soil (frost boils or mud hummocks) that make up the patterned ground features of the vegetation type, an indication that these soil features generated and maintained by frost churning have stabilized to some degree. We speculate that periodic stabilization would be consistent with lower soil moisture levels in the active layer of underlying Cryosolic soils, resulting from warmer, drier climatic conditions.

Key Words: Polargrass, *Arctagrostis latifolia*, Arctic Lupine,*Lupinus arcticus*, Arctic tundra, Herschel Island, Yukon Territory.

During the summers of 1985 and 1986 a 1:20 000 scale soil and vegetation mapping survey was conducted on Herschel Island (Smith et al. 1989), as part of a multi-disciplinary resource inventory. The island was established as a territorial park in 1987, as a result of a commitment made in the Inuvialuit Final Agreement, signed in 1984. Herschel Island lies off the north coast of the Yukon Territory in the Beaufort Sea (69'30" North, 139'00"West) approximately 250 km northwest of Inuvik, NWT (Figure 1). The island is composed of glacial ice-thrust marine sediments (Mackay 1959; Rampton 1982) with no bedrock control to the topography. The most recent estimate of the age of the glaciation that led to the formation of the island is approximately 30 ka (Duk-Rodkin 1999). Soils are composed primarily of silt and clay with minor sands and gravels. The upland soils of Herschel Island have an active layer that averages 30 to 50 cm thick overlying ice-rich permafrost. The tundra vegetation cover is primarily comprised of Cottongrass tussocks, prostrate shrubs, diverse forbs and other graminoids, whose distribution is controlled by soil moisture regime, exposure and degree of solifluction disturbance to the site (Smith et al. 1989).

Vegetation data were collected during a five-week field survey in July and August 1985 and a one-week verification field survey in July 1986. Plant species occurrence and cover data from approximately 125 plots were summarized by tabular analyses into 11 vegetation types based primarily on the dominance of species in each strata. The undulating to level upland portion of the island is dominated by three vegetation types. Level, uneroded surfaces are covered by "tussock tundra" dominated by Cottongrass *(Eriophorum vaginatum)* and a well developed moss layer dominated by *Sphagnum* species. Gently undulating surfaces associated with non-sorted patterned ground are dominated by a community of Arctic Willow *(Salix arctica)*, with a mat of Dryas *(Dryas integrifolia)* and Milk-Vetch *(Astragalus umbellatus)*. On gentle slopes where there is less patterned ground, willows *(Salix arctica* and *Salix reticulata)*, mosses and a diverse forb coverage including *Milk-Vetch (Astragalus umbellatus)*, Bistort *(Polygonum viviparum)*, Saxifrage (*Saxifraga hirculus)* and

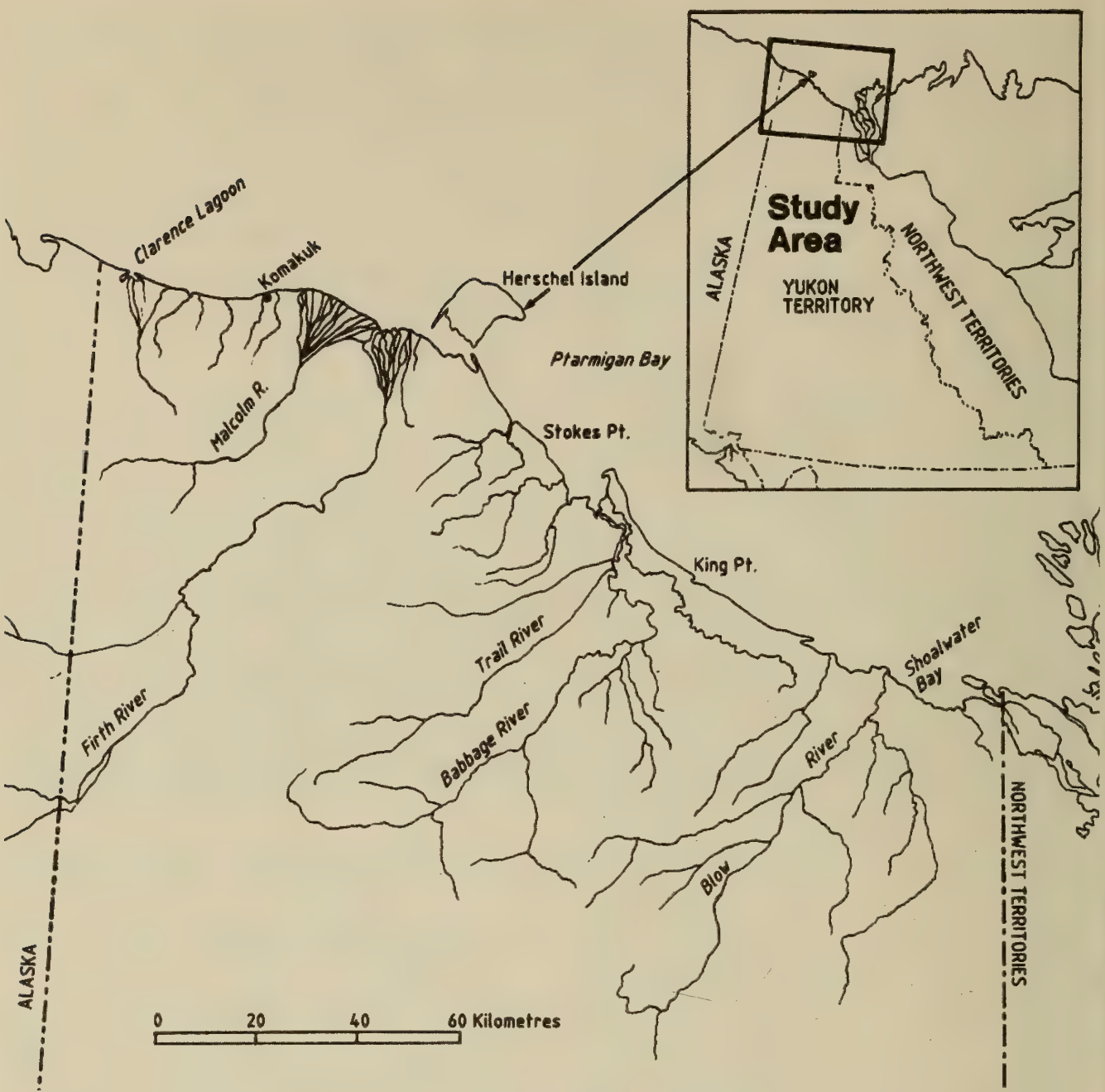

FIGURE 1. Location of study area, showing Yukon Territory (inset), Herschel Island and the adjacent mainland.

Coltsfoot *(Petasites* spp) is present. Eight other vegetation types (i.e. communities) were defined for the island that covered the wetland environments (e.g. low centre polygons, thermokarst ponds), and the marine foreshore environment as well as the actively eroding slopes (Smith et al. 1989) on the island.

In the summer of 1999 we returned to the island to set up vegetation monitoring plots as part of the International Tundra Experiment (ITEX) and had the opportunity to make observations on the general character of vegetation communities on the island. It became clear that very observable physiognomic changes due to species cover changes had occurred since 1985/1986 within at least one of the most widespread communities on the upland of the island. At first glance, much of the upland of the island appeared to be grassier than described in 1985 largely as a result of an apparent increase in the cover of *Arctagrostis latifolia*. Here we describe our initial observations of the nature of this change in cover.

Methods

In the 1985/1986 field survey, vegetation plots were selected within homogenous vegetation stands. All vascular and non-vascular plant species were recorded for occurrence and percent cover (in percentage classes) within a circular plot, approximately 20 metres in diameter. To quantify our initial visual impressions of cover change in the brief time on the island between 12 and 18 July 1999, we attempted to re-visit 1985 plot sites based on location points recorded on 1:10 000 black-and-white aerial pho-

tographs and site photographs from the original survey that we had with us. With a fair degree of confidence we located three sites, distributed around the island on a range of landform conditions associated with this vegetation type. On each of these sites, species occurrence and cover values were recorded by the senior author using the same plot sampling technique as used in the original survey.

Results and Discussion

The vegetation community showing the marked difference in cover, Arctic Willow/Dryas-Vetch, occurs on the undulating portions of the upland associated with patterned ground formation. A species list and their basal coverage based on 21 plot observations in 1985/1986 is given in Table 1. *Dryas integrifolia* was present on all sites and had an average cover value of 24%. *Salix* spp. coverage was 13% and present on most sites. Numerous additional forbs and graminoids were present in low to trace amounts. Sites classified as belonging to this type had 15 to 65% of bare soil produced by active non-sorted circle (frost boils) and net patterned ground associated with Orthic Turbic Cryosol soil formation (Smith et al. 1991). Bryophytes occur in the depressions between circles and can have total cover values from 10 to >20%. Moss species identified within this vegetation type include *Timmia austriaca, Drepanocladus uncinatus, Pogonatum alpinum, Hylocomium splendens* and *Philonotis fontana*. Many of these species are associated with calcareous substrates. Frost action in the soil tends to move calcareous soil parent materials to the surface and into the depressions between circles.

The 1999 cover values for graminoid species and one conspicuous forb, *Lupinus arcticus* are presented in Table 2. While such a small sample size does not allow for statistical comparisons between plot data from the two sample dates, visible changes in the vegetation community were observed. In each of the three sites, *Arctagrostis latifolia* cover value increased, in one case (site 004) from 1% cover to 5% cover, in a second case (site 014) from not present to 1% cover and in a third case (site 308) from 5% cover to 10%

TABLE 1. List of the shrubs, forbs, graminoids and lichens that make up the Arctic Willow/Dryas-Vetch type based on 21 plots in 1985/1986.

Layer	Species	Percent Occurrence	Percent Cover
Shrubs:	*Salix arctica*	75	9
	Salix reticulata	66	4
Forbs:	*Dryas integrifolia*	100	24
	Astragalus umbellatus	95	1
	Astragalus alpinus	61	2
	Lupinus arcticus	85	2
	Parrya nudicaulis	90	tr
	Myosotis alpestris	80	tr
	Pedicularis capitata	66	tr
	Senecio lindstroemii	70	tr
	Polgonum viviparum	61	tr
	Papaver spp.	70	tr
	Saxifraga spp.	66	tr
	Saxifraga punctata	52	tr
	Saussurea angustifolia	47	tr
	Oxytropis nigrescens	52	tr
	Pedicularis lanata	52	tr
	Draba spp.	60	tr
	Minuartia obtusiloba	52	tr
	Polygonum bistorta	42	tr
	Pedicularis spp.	60	tr
Graminoids:	*Carex* spp.	66	tr
	Luzula nivalis	47	tr
	Arctagrostis latifolia	47	1
	Poa spp.	42	tr
Lichens:	*Cetraria cucullata*	85	3
	Thamnolia subuliformis	84	3
	Alectoria ochroleuca	84	tr
	Cetraria islandica	57	tr
	Centraria nivalis	52	tr
	Dactylia arctica	52	tr
	Alectoria nigricans	47	tr

TABLE 2. Summary of observed cover changes in selected species from three sites belonging to the Arctic Willow/Dryas-Vetch vegetation community. Values in bold show increased species cover between 1985 and 1999 observations.

	% Species Cover[1]					
	Site 4 69°33.3'N, 139°09'W		Site 14 69°35.4'N,139°10.3'W		Site 308 69°37.2'N,139°01.6'W	
Plant Species Year	1985	1999	1985	1999	1985	1999
Graminoids						
Arctagrostis latifolia	**1**	**5**	–	**1**	**5**	**10**
Carex lugens	tr	tr	–	–	15	15
Luzula nivalis	tr	tr	–	–	1	1
Eriophorum angustifolium	1	1	–	–	tr	tr
Forbs						
Lupinus arcticus	–	**1**	–	–	**1**	**10**

[1] = not present, tr = trace (<1%)

cover. In 1985, this species was present on only 47% of sites classified as this type and with a 1% mean cover value. Similarly, *Lupinus arcticus* cover value increased markedly on two of the three sites inventoried. In one case it occurred where it did not exist in 1986 and on another increased in cover from 1% cover to approximately 10%. Other graminoids that occur within the plant community (sedge, cottongrass, bluegrass) did not appear to have changed cover values.

Based on a limited number of plots and traverse observations through the upland of the island, areas surrounding patterned ground exhibited the most dramatic increase of Polargrass cover which seems to have established ubiquitous cover within the Arctic Willow/Dryas-Vetch vegetation type. Most notable was the physiognomic change of a community initially characterized by prostrate shrubs and forbs, to one characterized by grass (Figure 2). Incidental observations were also made in other vegetation types on the uplands, eroded slopes and the marine foreshore; although some changes were observed, apparent change in cover among plant species appears to be relatively minimal and/or inconsistent.

The Arctic Willow/Dryas-Vetch vegetation type is the most widespread on the island where it is the dominant type on the gently sloping uplands that make up almost 50% of the island's total area (Smith et al. 1989). A change in vegetation structure and composition over this extent of the island may have ecological consequences for the Caribou (*Rangifer*

TABLE 3. Summary of temperature and precipitation deviations from Inuvik, NWT between 1985 and 1999 (data for 1995 and 1996 are missing). Based on the 1960–1990 normals, values for mean annual temperature is -9.5°C, annual precipitation is 257 mm, summer (June, July, August) mean temperature is 11.6°C and summer precipitation is 100 mm (Environment Canada 1993).

	Deviation from 30 year normal[1]			
Year	Annual mean temperature (°C)	Annual precip (mm)	Summer mean temperature (°C)	Summer precip (mm)
1985	+0.4	-91	-1.3	-69
1986	-0.6	-28	-0.1	-17
1987	+1.3	-2	+1.0	-16
1988	+1.4	-32	+1.4	-21
1989	+2.0	+29	+3.2	+16
1990	+0.1	-20	+0.6	-16
1991	+0.8	+39	-0.9	+23
1992	+0.5	+20	+1.0	-27
1993	missing	-8	missing	-25
1994	+1.3	+41	+2.9	+2
1997	+2.5	-6	+1.5	+18
1998	+4.9	-1	+3.1	+18
1999	+0.7	-34	+0.4	0

[1]Data supplied by William Miller, Environment Canada, Whitehorse, Yukon Territory.

FIGURE 2. Cover changes in the Arctic Willow/Dryas-Vetch vegetation type are illustrated from one site typical of the upland on Herschel Island. Figure 2a (above) was taken on 4 August 1985. Figure 2b (below) was taken from the same site on 16 July 1999. The graminoid cover in 1999 is composed predominantly of Polargrass *(Arctagrostis latifolia)* .

tarandus) and Muskoxen (*Ovibos moschatus*) that use the island. The numbers of Caribou and Muskoxen grazing on the island have varied over the last decade. It will be necessary to examine specific grazing behaviors in order to assess the extent to which faunal impacts on vegetation cover values are responsible for the observed changes.

We suspect that climatic variations over the two decades may be the most likely cause driving vegetation change. Unfortunately, there are no continuous weather data available for this period from the automated weather station on Herschel Island. Based on records from Inuvik in the Mackenzie Delta some 250 km to the east, the last 15 years have been remarkably warmer in the region and precipitation has been somewhat lower (Table 3). All but one year since 1985 have been warmer than the 30 year normal; 1998 recorded a deviation in annual mean temperature of almost 5.0°C and summer soil thaw was abnormally deep in the region (Wolfe et al. 2000). Nine of the 13 years for which data are available, show below normal annual precipitation. Responses of tundra vegetation to experimental and observed changes in climate on the north slope of Alaska indicate that elevated temperature can increase nutrient mineralization in the soil with a subsequent increase in plant nutrient availability (Chapin et al. 1995). Grasses are known to respond quickly to increased nutrient availability. Changes in plant biomass between 1985 and 1995 led Chapin et al. (1995) to conclude that regional climatic warming may already be altering the species composition of tundra in the Alaskan north slope region.

We also noted that bare ground (frost boils or mud hummocks) generated by cryoturbation processes in the soil, seems to be undergoing invasion by Polargrass and Arctic Lupine, an indication that these features have stabilized to some degree. We know that both the degree and intensity of cryoturbation in soil varies over several orders of time (Zoltai et al. 1978; Mackay and MacKay 1976). Periodic stabilization would be consistent with lower soil moisture levels in the active layer resulting from warmer, dryer climatic conditions and would favour the growth of opportunistic species like *Arctagrostis latifolia* and *Lupinus arcticus*. Therefore, while the environmental changes that seem to be taking place on Herschel Island may not be outside of the natural variability of soil and vegetation dynamics, understanding this variability is necessary in establishing a baseline for future ITEX monitoring on the island and in interpreting those observations. In addition to this long term monitoring, in the coming field seasons we will follow-up this initial observation of vegetation change with additional detailed plot work to quantify plant species and soil properties changes and determine the geographic extent of this phenomenon on upland plant communities in the region.

Acknowledgments

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Survey of Freshwater Mussels in the Petitcodiac River Drainage, New Brunswick

JOHN MARK HANSON and ANDREA LOCKE

Gulf Fisheries Centre, Department of Fisheries and Oceans, P. O. Box 5030, Moncton, New Brunswick, E1C 9B6, Canada

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Five species of freshwater mussels were collected in a survey of 66 sites in the Petitcodiac River system, New Brunswick. One tributary, the North River, was almost devoid of all species — apparently due to habitat degradation associated with poor agricultural practices. The Eastern Pearlshell (*Margaritifera margaritifera* Linnaeus 1758) was common in most of the running water portion of the river system and was the only species present at 22 sites. The Eastern Floater (*Pyganodon cataracta* Say 1817) was restricted to habitats with fine sediments in the main Petitcodiac River and the lower 2 km of the Little River, and in two reservoirs. The Eastern Elliptio (*Elliptio complanata* Lightfoot 1786) was common in areas of sand or fine gravel in slower-flowing sections of the main Petitcodiac River and the Anagance River but was absent from the Little and Pollett rivers and Turtle Creek. The Brook Floater (*Alasmidonta varicosa* Lamarck 1819) was locally common on sand and fine gravel substrates in the lower 6 km of the Little River and also occurred in widely scattered patches in the main Petitcodiac River. The Triangle Floater (*A. undulata* Say 1817) shared the same general distribution as the Brook Floater but we seldom found more than five individuals of it at any site.

Key Words: Mollusca, Unionidae, abundance, distribution, habitats.

North America has the highest diversity of freshwater mussels in the world, yet these molluscs represent the most threatened taxonomic group in North America (Williams et al. 1993; Primack 1998). There are 297 recognized species and subspecies in the USA and Canada, of which only 70 are considered to have stable populations. Although 53 species have been recorded in Canada (Williams et al. 1993; Metcalfe-Smith et al. 1998a), the conservation status of most freshwater mussel species in Canada has not been directly assessed by the Committee on Status of Endangered Wildlife in Canada (COSEWIC). Halting the decline in freshwater mussel populations requires knowledge of the current abundance and distribution as well as an understanding of habitat requirements of both the freshwater mussel species and the fish hosts necessary for completion of the life cycle. Assessing the status of freshwater mussel species in Canada is difficult because few comprehensive surveys of river systems have ever been conducted. A notable exception is the Lower Great Lakes Basin in Ontario, which is the site of ongoing assessments of a number of freshwater mussel species whose Canadian distribution is limited to this area (e.g., Metcalfe-Smith et al. 1998a,b; Staton et al. 2000; West et al. 2000). The Maritime Provinces also contain freshwater mussel species not found elsewhere in Canada. As with many parts of Canada, the published information needed to assess the status of the freshwater mussel fauna of the Maritime Provinces is almost non-existent.

Clarke (1981) listed 12 species of freshwater mussel in the Maritime Provinces. One of these, the Dwarf Wedgemussel (*Alasmidonta heterodon*) is now considered extirpated in Canada (Hanson and Locke 2000). The conservation status in Canada of the remaining 11 species has not been assessed by COSEWIC. The American Fisheries Society has listed two of these 11 species as threatened (Brook Floater *Alasmidonta varicosa*, Yellow Lampmussel *Lampsilis cariosa*), and three are listed as of special concern (Triangle Floater *Alasmidonta undulata*, Eastern Pearlshell *Margaritifera margaritifera*, Tidewater Mucket *Leptodea ochracea*) (Williams et al. 1993). The other five unionid species found in the Maritimes are the Alewife Floater (*Anodonta implicata*), Eastern Lampmussel (*Lampsilis radiata radiata*), Eastern Floater (*Pyganodon cataracta*), Newfoundland Floater (*Pyganodon fragilis*), and Creeper (*Strophitus undulatus*). The Eastern Pearlshell is unique among North American freshwater mussels because it also occurs in Europe. In Europe, this species is listed as endangered or extirpated over much of its range (Cosgrove et al. 2000).

The current distributions of freshwater mussel populations in Maritime waters likely differ substantially from those described by Clarke decades ago (1981). The data summarized by Clarke were obtained from preliminary surveys (mostly unpublished) conducted in the 1950s and early 1960s. Published information on distributions of freshwater mussels in New Brunswick is very rare (e.g., Athearn 1961) while a small number of published studies exist for rivers in Nova Scotia (Athearn and Clarke 1961; Clarke and Rick 1963). However, these surveyors seldom sampled more than two or three sites per river and consequently may have missed species that were present at low densities or in very specific habitats. We are not

aware of any studies of freshwater mussels on Prince Edward Island. Environmental conditions have also changed a great deal since the studies mentioned above. In the past 40 or 50 years, many dams and causeways have been built in the Maritimes (Wells 1999). Blockage of rivers or impoundment is one of the major causes of loss of freshwater mussel populations as it usually results in drastic habitat changes above and below the dam and the inability of fish hosts to pass by the obstruction (Bogan 1993; Watters 1995; Vaughn and Taylor 1999). In addition, there is the possibility that new species of freshwater mussel have become established in Maritime rivers, as a result of numerous introductions of freshwater fishes for sport fishing, some of which may have carried glochidia.

During a previous study aimed at assessing the conservation status of the Dwarf Wedgemussel (Hanson and Locke 2000), we conducted a thorough survey of the entire freshwater portion of the Petitcodiac River system. To the best of our knowledge, this was the first time an entire river system in the Maritime Provinces was extensively surveyed for freshwater mussels. This report provides a baseline study to document the relative abundance and distribution of freshwater mussels in the Petitcodiac River system based on surveys conducted during 1997–2000.

Study Site

The Petitcodiac River is located in southeastern New Brunswick at the head of the Bay of Fundy (Figure 1). In 1968, the Petitcodiac River estuary was blocked by a causeway (46° 04.13' North; 64°48.62' West) located 21 km below the former head of tide, and a long, narrow, freshwater headpond was formed. Our study area included the headpond and the drainage basin upstream of the causeway. The freshwater river and its five main tributaries (Anagance, Little, North, and Pollett rivers and Turtle Creek) have a combined length of 175 km and drain a watershed area of 1360 km^2. Mean flow at the causeway is 27.3 m^3/s (range 0.35 to 729 m^3/s) (Caissie 2000). Turtle Creek was dammed to form a municipal drinking-water reservoir 10-km upstream of the mouth in 1982, and no fish passage facilities were provided. Most of the small dams that were present in the freshwater tributaries at various times during the past century have been removed, but several small, derelict, impoundments remain in the headwaters of the Little and Pollett rivers.

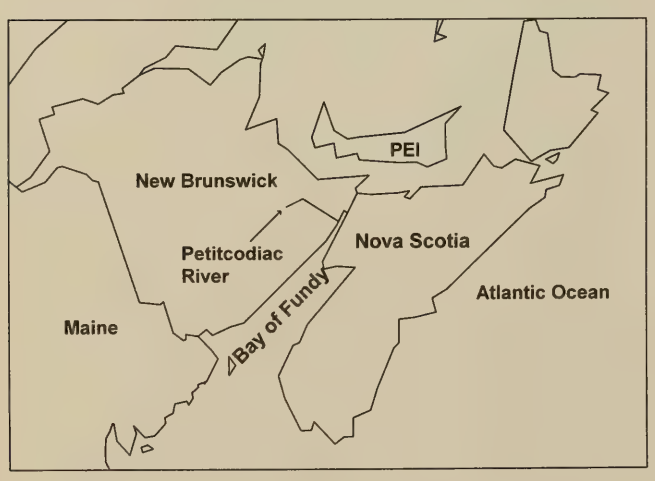

FIGURE 1. Location of the Petitcodiac River system in Canada.

The presence of the causeway has resulted in the loss of many of the anadromous fish species that may have served as hosts for the glochidial stages of freshwater mussel species inhabiting the Petitcodiac River system. Two fishways that were constructed to permit passage of diadromous fishes past the causeway have been ineffective and virtually all species have been eliminated or severely diminished (Beaulieu 1970; Wells 1999). Spawning runs of Atlantic Salmon (*Salmo salar*), American Shad (*Alosa sapidissima*), Striped Bass (*Morone saxatilis*), and Atlantic Tomcod (*Microgadus tomcod*) no longer occur. A very small population of Atlantic Salmon has been maintained by stocking. The anadromous species that continue to reproduce in the river include Sea Lamprey (*Petromyzon marinus*), Brook Trout (*Salvelinus fontinalis*), Rainbow Smelt (*Osmerus mordax*), Alewife (*Alosa pseudoharengus*), Blueback Herring (*A. aestivalis*), and Fourspine Stickleback (*Apeltes quadracus*). The fish community of the headpond and most of the river system is now dominated by White Sucker (*Catostomus commersoni*), American Eel (*Anguilla rostrata*), Fourspine Stickleback, Ninespine Stickleback (*Pungitius pungitius*), and at least six minnow species (Cyprinidae). White Perch (*Morone americanus*) are becoming increasingly common in the headpond and in the running waters of the river system. In recent years, Chain Pickerel (*Esox niger*), Brown Bullhead (*Ameirus nebulosus*), and Smallmouth Bass (*Micropterus dolomieui*) have been illegally introduced into the headpond and its tributaries and their populations are increasing rapidly (Locke 1999).

Methods

We conducted a watershed-wide survey of freshwater mussels in the Petitcodiac River and its tributaries from 23 July to 21 October 1997, 2 June to 28 August 1998, and 14 to 20 June 2000. We used visual searches (by wading) to investigate 52 lotic sites and two headwater reservoirs in the system. Locations surveyed in 1997 and 1998 are listed in Hanson and Locke (2000); those surveyed in 2000 are listed in Table 1. Visual searches were conducted by surveying the full width of the river with a team of two to three searchers. In 1997, we conducted timed searches (one to two hours, two searchers). All sites visited during 1997 were also surveyed during

TABLE 1. Summary of sites visually surveyed for freshwater mussels in the Petitcodiac River watershed, in 2000. Positions of sites were obtained from Energy, Mines and Resources Canada 1:50 000 scale topographic maps of Moncton (21-I/2, edition 4), Salisbury (21-I/3, edition 3), Petitcodiac (21-H/14, edition 3), and Hillsborough (21-H/15, edition 3). Sites surveyed in 1997–1998 are listed in Hanson and Locke (2000).

River	Site (access point)	Latitude (DD MM)	Longitude (DD MM)	Distance Searched (m)
Petitcodiac River	Railroad Bridge	45 58.36	65 07.95	500
Anagance River	Town of Anagance	45 52.46	65 15.55	60
Turtle Creek	Foot bridge	46 01.24	64 53.55	200
Turtle Creek	Jonah Road	45 56.43	64 52.05	600
Turtle Creek	Tower Road	45 57.59	64 52.77	300
Little River	Blackwood Lake	45 45.56	64 57.74	300
Pollett River	The Glades	45 56.68	65 05.28	500

1998 and our assessment of relative abundance was based on the 1998 and 2000 surveys. In 1998 and 2000 (usually three searchers), we used a 50 m tape measure or a metered thread-dispensing device (Chainman II, Chainman Inc., Vancouver, British Columbia) to measure the distance searched, and did not restrict the time spent at each location. The stream length searched ranged from 60 to 1500 m (median 518 m; quartiles 300 and 750 m; total stream length searched 29.3 km) and stream width varied between 3 and about 50 m. All stream banks and sand or gravel bars were carefully searched for empty shells. We also carefully examined shells in all Muskrat (*Ondatra zebithicus*) middens encountered in the watershed (Meike and Hanson 2000). We searched the shorelines of two small impoundments in the headwaters of the Little River for shells left on muskrat middens and also searched the bottom to a depth of 1.5 m using the same visual search method as used in running water sites. Water clarity was excellent at all locations. All submersed habitat was searched visually and by digging in sand and gravel around rocks and boulders. Locations with large deposits of sand and fine gravel were sampled with a 30 cm wide push net (each sample represented about 0.25 m^2, to a depth of 5–6 cm), and sieved through the 6 mm mesh netting. This method was even more sensitive than timed searches for detecting rare species as indicated by the fact that very small juveniles (as small as 7 mm shell length) of several freshwater mussel species were collected. These small specimens were not detectable by standard timed-search methods. We defined relative abundance at each site as not found, rare (< 0.01 unionids per site), scarce (0.01 to 0.1 unionids/m^2), common (0.1 to 1 unionids/m^2), or abundant (> 1 unionids/m^2). In most cases, living animals were identified to species and replaced. Some specimens were retained for voucher purposes or length-frequency analyses.

Twelve stations in the main Petitcodiac Headpond were sampled during August of 1997, 1998, and 1999. Sediments were collected with a 23 × 23 × 23 cm Ekman dredge, 10 dredge hauls per sample, three samples at each of 1, 2, 3, and > 4 m depths. Sediments were washed on a 6-mm sieve. All animals collected were taken to the laboratory where, as part of a separate study, we recorded age, shell length, shell weight, and viscera weight.

The common and scientific names of freshwater mussels used in this study followed Turgeon et al. (1998). Voucher specimens have been deposited at the New Brunswick Museum, Saint John, N.B.

Results

Five species of freshwater mussels were collected in the Petitcodiac River system: Eastern Pearlshell (*Margaritifera margaritifera*), Brook Floater (*Alasmidonta varicosa*), Triangle Floater (*A. undulata*), Eastern Elliptio (*Elliptio complanata*) and Eastern Floater (*Pyganodon cataracta*). Much of the North River was not suitable habitat for any freshwater mussel species principally due to poor agricultural practices. Above the agricultural areas of the North River, the two sites located furthest upstream did not appear to be degraded and the habitat closely resembled the middle portion of the Little River where the Eastern Pearlshell was common. Nevertheless, freshwater mussels were not found at either of these sites. In addition, no freshwater mussels were found in one of the small headwater reservoirs on the Little River. Freshwater mussels were found at virtually all other sites.

The Eastern Pearlshell was widespread in lotic waters of the system (Figure 2) but absent from the Petitcodiac headpond and the two small reservoirs on the Little River. It was common to abundant in parts of the main Petitcodiac River, lower Anagance River, lower Pollett River, Little River, and Turtle Creek above the Turtle Creek Reservoir. We found clear evidence of recent reproduction (individuals < 25 mm long) in all but the Turtle Creek sites. The Eastern Pearlshell was scarce in most of the Pollett River and in Turtle Creek below the drinking-water reservoir. Single specimens were collected at three sites on the North River. The Eastern Pearlshell

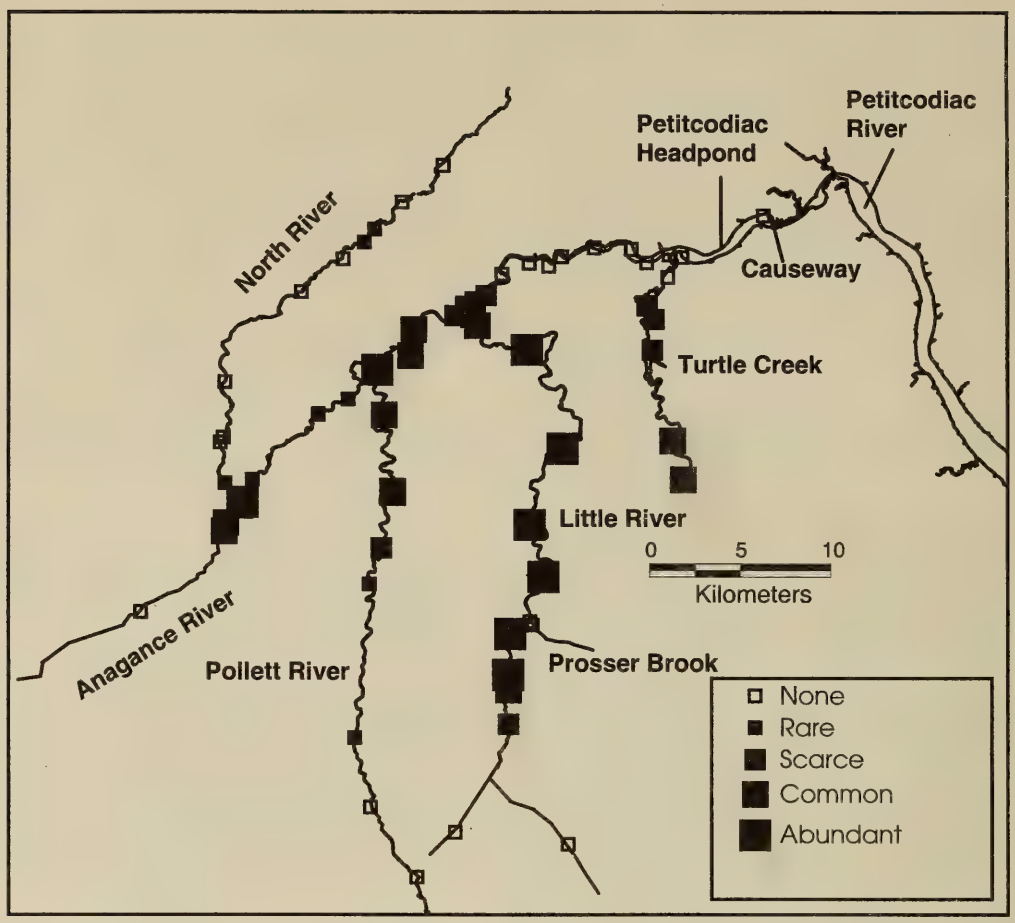

FIGURE 2. Distribution and relative abundance of the Eastern Pearlshell (*Margaritifera margaritifera*) in the Petitcodiac River and tributaries upstream of the Petitcodiac causeway.

occurred in single species beds in 22 of the 42 locations where it occurred, mainly in the Pollett River, Turtle Creek, and most of the Little River. The freshwater mussel beds in the lower Anagance River usually contained equal numbers of Eastern Elliptio and Eastern Pearlshell. The Brook Floater was the species most often found with Eastern Pearlshell in sand and gravel sites in the main Petitcodiac River and Little River.

The Eastern Floater was associated with reservoirs and with lotic habitats of reduced current speed (Figure 3). It was the only species collected in the one headwater reservoir of the Little River that contained mussels, and it overwhelmingly dominated the freshwater mussel community of the Petitcodiac Headpond. Large numbers of Eastern Floater occurred in the lower, more lentic, half of the Petitcodiac Headpond but it was rare in the narrow, steep sloped, upper half of this impoundment. The sediments in the areas of high Eastern Floater abundance in both reservoirs were typically composed of soft mud or soft mud overlying hard clay. Finally, small numbers of Eastern Floater were collected from mud or silt substrates in quiet backwaters of the main Petitcodiac and lower Little Rivers and in two sites of the North River. We found clear evidence of recent reproduction (individuals < 15 mm long) in all sites except those in the North River. This species was absent from the Pollett River, most of the Little River and Turtle Creek, and the Anagance River.

The Eastern Elliptio was found in slow-running water on sand or silty sand bottoms in the main Petitcodiac and Anagance rivers (Figure 4), usually in dense beds near the banks. The Eastern Elliptio usually represented over 95% of the freshwater mussels present in these beds. We found clear evidence of recent reproduction (individuals < 15 mm long) in all sites occupied by Eastern Elliptio in these two rivers. Small numbers of Eastern Elliptio were found at the sites supporting mussels in the North River, usually where a stream entered the river or in springs, but there was no indication of recent reproduction. The Eastern Elliptio was not present in either reservoir on the Little River but a few specimens were collected along with large numbers of Eastern Floater on three sandbars in the main Petitcodiac headpond. The Eastern Elliptio was absent from the Little and Pollett rivers, and Turtle Creek. The sediments in these rivers ranged from coarse sand to cobble and boulder with moderate to rapid water current.

The Brook Floater was found only in running water sections of the Petitcodiac River system

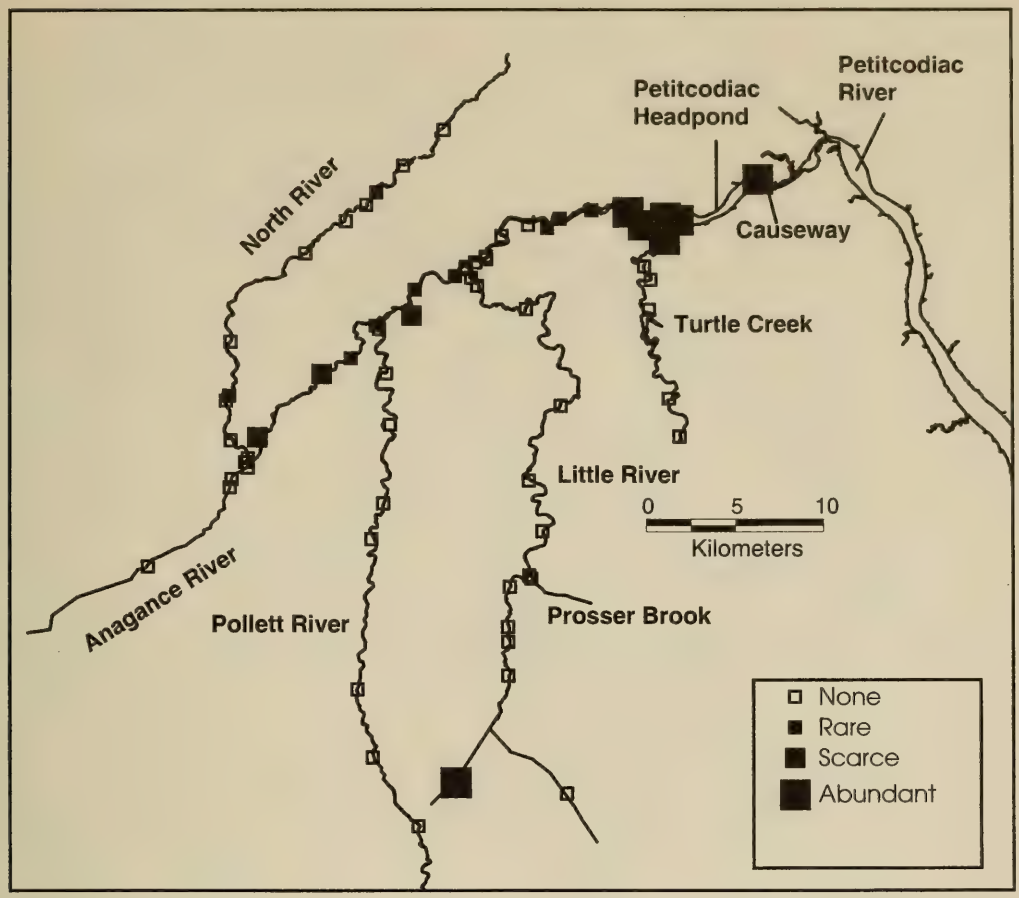

FIGURE 3. Distribution and relative abundance of the Eastern Floater (*Pyganodon cataracta*) in the Petitcodiac River and tributaries upstream of the Petitcodiac causeway.

(Figure 5). The Brook Floater was found in locally high abundance in beds located in backwaters of sand or gravel bars in the lower 6 km of the Little River and in small groups (5 to 20 animals) in pockets of coarse sand behind large boulders. Small groups of Brook Floater were collected in similar habitats in the main Petitcodiac River. This species was not found in the Pollett or Anagance rivers, most of the North River, or in Turtle Creek. We found clear evidence of recent reproduction (individuals < 15 mm long) at all sites occupied by this species except those in the North River.

The distribution of Triangle Floater was almost identical to that of the Brook Floater except that it was very rare at all locations (Figure 6). We never collected more than five living Triangle Floaters at any site. This species was very rare in the Petitcodiac River and was not found in the Pollett or Anagance rivers. Occasional specimens were collected in the lower 6-km section of the Little River. We found five living individuals in a spring in the North River and single specimens at four other sites. No specimens were collected in the running water portion of Turtle Creek but one living animal was collected on a sand bar in the flooded (as part of the main Petitcodiac Headpond) lower section of the creek. We found no evidence of recent reproduction (individuals < 15 mm long) by this species except at one site in the Little River. The Triangle Floater was rare throughout the drainage and it is possible that we overlooked small individuals or mistook them for very small Eastern Elliptio.

Discussion

Five species of freshwater mussels were collected in the Petitcodiac River system, but only two of these, the Eastern Elliptio and Eastern Floater, are considered by the American Fisheries Society to have stable conservation status (Williams et al. 1993). The Dwarf Wedgemussel was once common in the Petitcodiac and North Rivers but was eliminated from the system following completion of the Petitcodiac causeway (Hanson and Locke 2000). The Canadian range of the species was restricted to the Petitcodiac River, and the Dwarf Wedgemussel is now considered extirpated from Canada. The conservation status in Canada of the five species remaining in the watershed has not been determined by COSEWIC.

There is little published information on the mussel fauna of the Petitcodiac River system; hence, it is not clear whether the abundance and distribution of the species documented in this study represent a stable situation or one in transition. Each of the extant

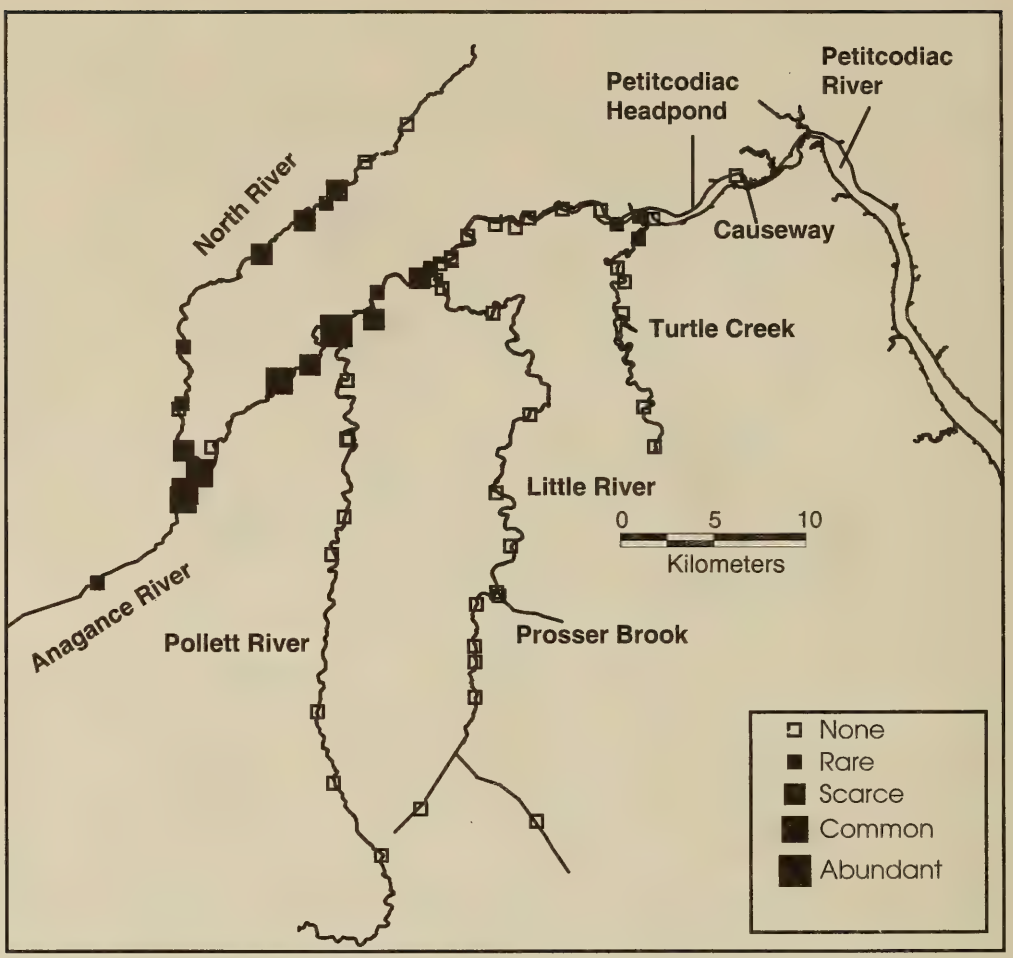

FIGURE 4. Distribution and relative abundance of the Eastern Elliptio (*Elliptio complanata*) in the Petitcodiac River and tributaries upstream of the Petitcodiac causeway.

species in the Petitcodiac system, however, has unique life history characteristics and relatively well defined habitat distributions that can be used to evaluate the risk to persistence of the species in the system. Under normal conditions, adult freshwater mussels have low natural mortality rates, although their sedentary lifestyle renders them susceptible to a number of anthropogenic threats. These threats include the physical effects of habitat degradation (e.g., conversion of riffle habitat into still water), over-harvesting, anoxia, metal contamination, and introduction of encrusting competitors (e.g., the Zebra Mussel, *Driessena polymorpha*) (Nalepa et al. 1991; Bogan 1993; Blalock and Sickel 1996; Ricciardi et al. 1998; Sparks and Strayer 1998). In the absence of these effects, events at early life stages largely determine the abundance and distribution of freshwater mussels in a water body. Although adult freshwater mussels release tens of thousands to millions of glochidia, only a very small fraction of them ever successfully attach to fish and survive to the benthic juvenile stage (Young and Williams 1983; Jansen and Hanson 1991; Buddensiek 1995). The distribution of the freshwater mussel species is subsequently determined by (1) sediment characteristics appropriate for the settling larvae, and (2) access by the host fish to the habitat. If the host fish can not enter a stretch of water, the freshwater mussel species will not be found there (Watters 1992; Graf 1997; Haag and Warren 1998). This is why the blockage of streams and rivers is a serious threat to the persistence of freshwater mussel populations worldwide.

The Eastern Pearlshell is listed as an endangered species in Europe (Bauer 1983; Cosgrove et al. 2000) and the American Fisheries Society lists it of special concern in Canada and the USA (Williams et al. 1993). The habitat requirements (clean running water over coarse sand, gravel, or cobble and gravel bottom) are relatively well studied for the Eastern Pearlshell (Bauer 1992; Hastie et al. 2000) and suitable habitat is widely available in the Petitcodiac River Drainage. Unfortunately, the populations in the Petitcodiac River Drainage appear destined for extermination due to reproductive failure. The principal fish hosts for the glochidial stage are Atlantic Salmon, Brown Trout and, possibly, Brook Trout (Athearn and Clarke 1961; Smith 1976; Bauer 1987; Cunjak and McGladdery 1991). Atlantic Salmon and Brook Trout occur in the Petitcodiac system. In the current study, there clearly had been recent reproduction of Eastern Pearlshell in the Little River and parts of the Pollett and Petitcodiac

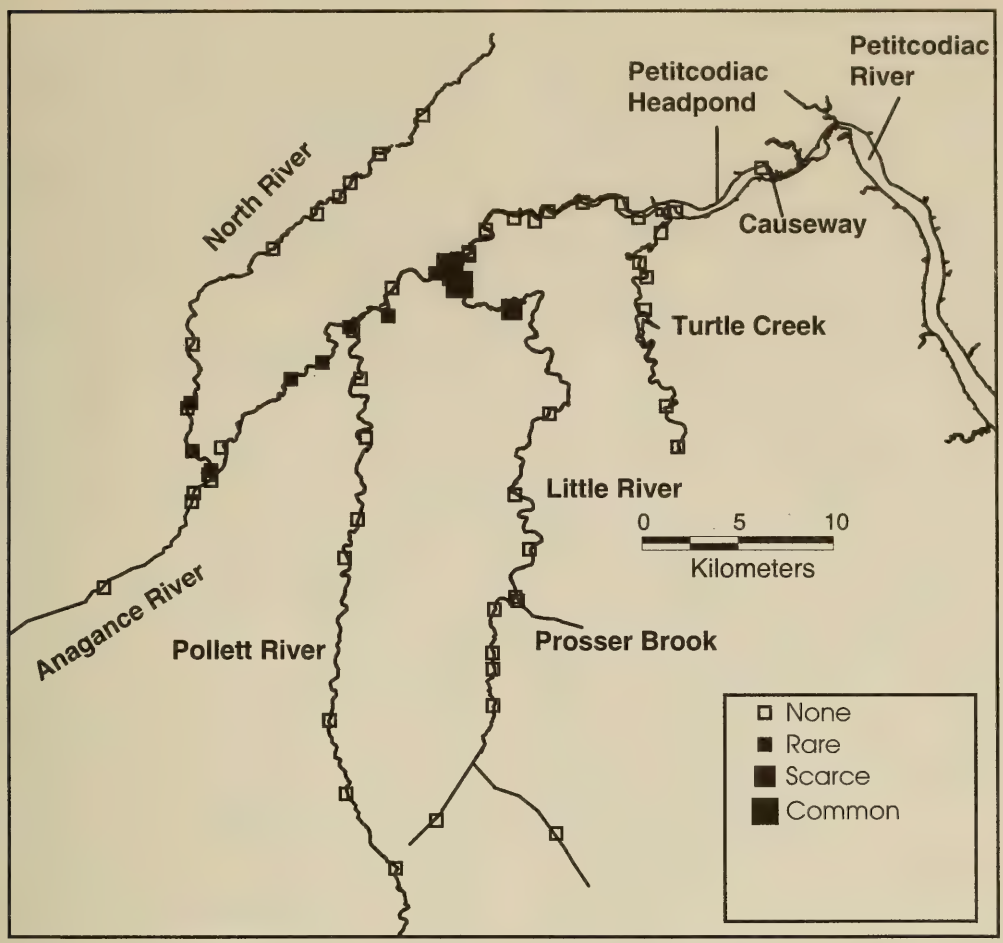

FIGURE 5. Distribution and relative abundance of the Brook Floater (*Alasmidonta varicosa*) in the Petitcodiac River and tributaries upstream of the Petitcodiac causeway.

rivers, most likely due to the large numbers of Atlantic Salmon parr and smolts stocked in the late 1980s and early 1990s. Areas of Turtle Creek that have not received plantings of salmon for 30 years, however, showed no signs of reproduction — all animals that we examined during our June 2000 survey (> 1000 individuals) were at least 80 mm long and most were > 100 mm long. Although Brook Trout were present in Turtle Creek, they either are not common enough to permit reproduction or this particular population of Eastern Pearlshell does not use Brook Trout as a glochidial host. In the case of the Petitcodiac River drainage, it is clear from the numerous failed attempts at stocking that Atlantic Salmon will never re-establish breeding populations as long as the causeway acts as a barrier to migration. Stocking activities have now ceased. Consequently, the Eastern Pearlshell populations in the Petitcodiac River system (similar to many other populations in North America) are functionally extirpated because reproduction is no longer possible due to the disappearance of the glochidial host fish. Non-reproducing populations of Eastern Pearlshell will likely persist for decades, however, because individuals can live about 100 years (Bauer 1983, 1992).

The Eastern Floater is considered by the American Fisheries Society to have stable conservation status in Canada and the USA (Williams et al. 1993). The Eastern Floater populations in the Petitcodiac River system do not appear to be threatened by current water management practices. In fact, this species arguably has benefited from formation of reservoirs in the drainage basin. The preferred habitat of the Eastern Floater is lakes, ponds, and slow moving streams — usually on sand or mud bottoms, and this is often the only species found in soft muddy habitats (Athearn and Clarke 1961). Reservoir construction in the Petitcodiac drainage has provided this soft muddy habitat in at least three impoundments but freshwater mussels are only present in two. One headwater reservoir has no means of fish passage and was devoid of freshwater mussels. In contrast, the second headwater reservoir has a functional fishway and supports a population of Eastern Floater. Lastly, the main Petitcodiac Headpond has had a history of colonization and population extermination due to various unsuccessful attempts to provide passage for Atlantic Salmon through the causeway. As recently as 1988, the entire population of Eastern Floater was killed when the headpond filled with salt water at each high tide. Drawdowns in 1998 and 1999 exposed the entire littoral zone to air and killed all freshwater mussels in

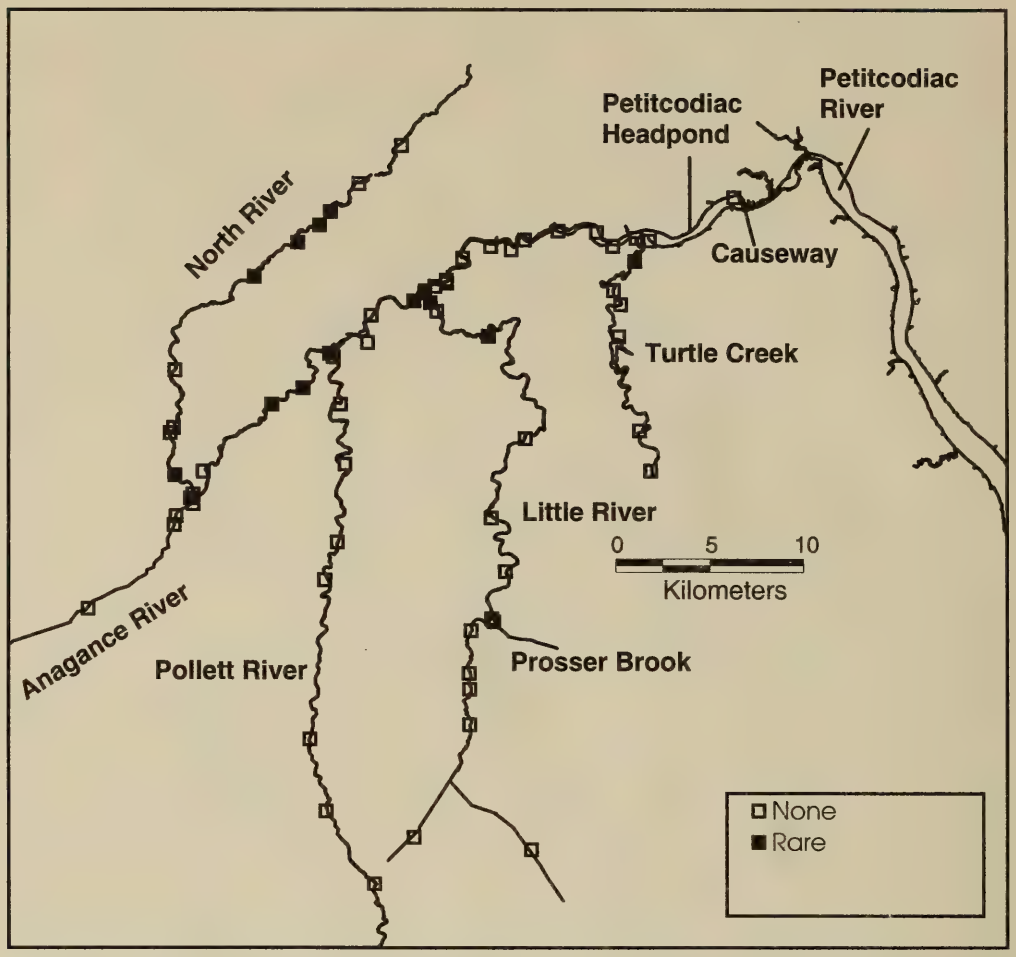

FIGURE 6. Distribution and relative abundance of the Triangle Floater (*Alasmidonta undulata*) in the Petitcodiac River and tributaries upstream of the Petitcodiac causeway.

the headpond except those living in the sublittoral zone (S. Richardson, J. M. Hanson, and A. Locke, unpublished data). The ability to colonize these impoundments requires a highly mobile host fish for the glochidia. The known hosts for Eastern Floater include Threespine Stickleback (*Gasterosteus aculeatus*), White Sucker (*Catostomus commersoni*), Pumpkinseed (*Lepomis gibbosus*), and Common Carp (*Cyprinus carpio*) (Wiles 1975; Clarke 1981; Threlfall 1986). Threespine Stickleback and White Sucker are recorded in the drainage but only White Sucker is abundant at all sites where Eastern Floater was collected. Indeed, White Sucker is common throughout all of the drainage but habitat requirements probably limit the distribution of the Eastern Floater, which was absent from moderate- to fast-running water and coarse substrate.

The American Fisheries Society also considers the Eastern Elliptio to have stable conservation status in Canada and the USA (Williams et al. 1993). The populations of Eastern Elliptio in the Petitcodiac River system do not appear to be threatened. The only known glochidial hosts of the Eastern Elliptio are Yellow Perch (*Perca flavescens*) and Banded Killifish (*Fundulus diaphanus*) (Matteson 1948; Wiles 1975; Paterson 1985). Yellow Perch do not occur in the Petitcodiac system while Banded Killifish were observed at all sites where Eastern Elliptio was found. Banded Killifish were also observed at many sites where Eastern Elliptio was absent, especially in the main Petitcodiac Headpond. Similar to the Eastern Floater, the availability of suitable substrate appears to be limiting distribution of Eastern Elliptio rather than the distribution of the fish host. The Eastern Elliptio is generally most common in slow or still waters on sand (plus silt) or sandy gravel whereas the bottom of the main headpond is mostly soft silt, which is not the preferred habitat of this species (Matteson 1948; Ghent et al. 1978; Amyot and Downing 1991).

The Brook Floater is listed by the American Fisheries Society as "threatened" in Canada and the USA (Williams et al. 1993) because it has disappeared from many locations where it formerly was found (Clarke 1986; Counts et al. 1991; Strayer and Fetterman 1999). The conservation status in Canada has not been assessed by COSEWIC but this might be a candidate species for immediate assessment under the criteria listed by Metcalfe-Smith et al. (1998). In Canada, this species is not reported outside of New

Brunswick and Nova Scotia, where it is rare. Within New Brunswick, the Brook Floater is listed as rare and only occurring in the Petitcodiac River (Clayden et al. 1984). This limited distribution is misleading because little survey information has been published for New Brunswick waters. Indeed, Athearn (1961) reports it was found in the Renous River, a tributary of the Miramichi River and additional surveys may show it is widespread within the province. The Brook Floater was collected at only four of over 180 locations searched in Nova Scotia during the 1950s and early 1960s, and it was not common at any of them (Athearn and Clarke 1961; Clarke and Rick 1963). It is unknown whether any of these previously identified populations persist because there have been no large-scale surveys conducted since then. The distribution of Brook Floater in the Petitcodiac River Drainage was patchy but their persistence does not seem to be threatened by reproductive failure because we observed specimens < 15 mm long at several locations. This species seems to have fairly well defined habitat requirements that limits its distribution in the Petitcodiac River Drainage. It requires running water and sand or sandy gravel substrate (Athearn and Clarke 1961; Strayer and Ralley 1993) and these were the only areas where we found Brook Floater. Not all suitable habitat supported the species. Much of the upper Little River consists of superficially suitable habitat but the only species found was Eastern Pearlshell. This suggests that the host fish for Brook Floater does not ascend into headwaters of rivers; however, the glochidial host for Brook Floater is unknown. Based on the distribution of Brook Floater in the Petitcodiac River drainage, the host species would appear to be an anadromous fish. The fish species that best match the distribution of Brook Floater in the Petitcodiac River system as well as across the whole species distribution are Alewife (original range) and Blueback Herring, and these are the species that we recommend be studied first as potential hosts. To date, both fish species persist in the Petitcodiac River drainage and it is habitat destruction due to poor agricultural practices that is threatening some unionid populations (but see Muskrat predation below).

The conservation status of the Triangle Floater in the Canada and the USA is listed as of "special concern" by the American Fisheries Society (Williams et al. 1993). We are unable to conclude whether the Triangle Floater is likely to persist in the Petitcodiac River Drainage. Throughout its distribution it is described as uncommon in some areas and locally common in others (Athearn and Clarke 1961; Clarke 1986; Strayer and Ralley 1991). The host species for the Triangle Floater have not been determined. The Triangle Floater occurs in the Trent-Severn and Ottawa River systems in Ontario (Clarke 1981; Metcalfe-Smith et al. 1998a); therefore, at least one fish host is not anadromous. Although it clearly occurs in lakes (Metcalfe-Smith and Green 1992), the Triangle Floater was not found in any of the reservoirs in the Petitcodiac System. We encountered so few Triangle Floaters in our survey that it might be questionable whether this species attained a sufficiently large local concentration to permit fertilization of eggs except that the species appears to be a functional hermaphrodite (Kat and Davis 1984).

While we are confident that we detected all species currently present in the system we are puzzled by the absence of the Alewife Floater (*Anodonta implicata*). The Alewife Floater is usually found in low gradient coastal rivers and stable coastal ponds (Strayer and Ralley 1991). The Alewife Floater is widespread in New Brunswick and parts of Nova Scotia (Athearn 1961; Athearn and Clarke 1961; Clarke and Rick 1963; Kat and Davis 1984), and there are large numbers of Alewife (the principal glochidial host) in the Petitcodiac system; hence, we expected it to be present. Whether it formerly was present and eliminated due to construction of the Petitcodiac Causeway can not be resolved due to a lack of published records on the mussel fauna present in the system prior to causeway construction in 1968.

Habitat degradation is a common threat to all unionid species in the Petitcodiac River system. The North River in particular has been strongly affected by poor agricultural practices. Habitat degradation was extensive. The sediment in some areas was black in colour and released methane and hydrogen sulfide gas when disturbed. Cultivation of fields extended to within 2 to 3 m of the bank and in many places there were drainage ditches and pipes emptying directly into the river. In other areas, fences were built across the river to allow cattle full access to the river, resulting in destruction of the stream banks, elimination of shoreline vegetation, erosion, and deposition of fecal material directly into the river. Finally, macrophyte growth was excessive in many areas and the plants themselves and the substrate were thickly coated with algae, i.e., conditions under the plants were anoxic. Of the species present in the Petitcodiac River system, Eastern Elliptio is considered to be most tolerant of degraded environmental conditions (Strayer and Ralley 1991). Hence it is not surprising that, when small patches of freshwater mussels occurred in the North River, the Eastern Elliptio was the main species collected.

Muskrats (*Ondatra zibethicus*) are the only mammalian predator (other than man) that kills large numbers of adult freshwater mussels (Hanson et al. 1989; Neves and Odom 1989; Tyrell and Hornbach 1998). This predation tends to be localized and does not threaten the existence of populations of endangered freshwater mussels unless an area of high muskrat feeding coincides with a remnant population of an endangered species (Neves and Odom 1989; Bruen-

derman and Neves 1993; Hoggarth et al. 1995). Muskrat predation is not currently widespread in the Petitcodiac watershed and tends to focus on the most abundant mussels of large body size. The species consumed in the Petitcodiac in 1997 and 1998 were Eastern Pearlshell and Eastern Floater (Meike and Hanson 2000). We have since discovered several Muskrat middens adjacent to an extensive mussel bed dominated by Eastern Elliptio, which was the only species eaten. In addition, we discovered a single Muskrat midden adjacent to the largest single concentration of Brook Floater in the watershed. This midden contained shells of over 90 Brook Floater but we counted over 300 living animals in the River. Nevertheless, this observation supports earlier reports that Muskrats can be a threat when the predation corresponds with a location where a threatened or endangered species happens to be locally abundant.

In summary, we detected five freshwater mussel species in the Petitcodiac River Drainage, and one species known to be present in the early 1960s is extirpated (Hanson and Locke 2000). The current study is the first to clearly document the relative abundance and distribution of the entire freshwater mussel fauna in any Maritime Province river. In order to protect the integrity of our freshwater ecosystems in the Maritimes, it is critical that we know what species are present now and conduct regular surveys on key water bodies to assess the health of the populations and their habitats, and to monitor for the arrival of invaders (e.g., Zebra Mussels). Without comprehensive surveys, it is impossible to determine whether distributions have changed or abundance declined over time in this the most threatened taxon in North America. Native freshwater mussels do not play a major commercial role in Canadian waters, federal endangered species legislation (at time of writing) is lacking, and the group is not "popular" or well known to the public. As a result, there is little incentive to study or conserve freshwater mussels in Canadian waters; consequently, further species extirpations are inevitable.

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Notes

Three New Taxa and a Summary of the Mustard Family, Brassicaceae (Cruciferae), in Canada and Alaska

GERALD A. MULLIGAN[1]

1600 Apeldoorn Avenue, Ottawa, Ontario, K2C 1V5 Canada
[1] Formerly Scientist and Institute Director, Research Branch, Agriculture Canada, Ottawa, Ontario K1A 0C6 Canada

Mulligan, Gerald A. 2001. Three new taxa and a summary of the species in the mustard family, Brassicaceae (Cruciferae) in Canada and Alaska. Canadian Field-Naturalist 115(2): 341–342.

Three taxa of the mustard family (Brassicaceae/Cruciferae) are validated: *Descurainia incisa* var. *viscosa*, *Smelowskia johnsonii*, and *Smelowskia media*. These taxa are among those already included in a Key to the Brassicaceae (Cruciferae) of Canada and Alaska, the genera of which are summarized. A key to the genus *Smelowskia* is given.

Key Words: Brassicaceae, Cruciferae, key, taxa, genera, *Descurainia incisa* var. *viscosa*, *Smelowskia johnsonii*, *Smelowskia media.*

A key to 248 taxa in 58 genera of the Brassicaceae (Cruciferae) of Canada and Alaska appears on the internet site *http://res2.agr.ca /ecorc/cwmt/brasskey/index.htm*. It includes the type species of each genus, pertinent synonyms, general distribution, and information on the native or naturalized status of each taxon. The family is represented in Canada by the following genera (the number of taxa in each genus appears in brackets): *Alliaria* (1), *Alyssum* (4), *Aphragmus* (1), *Arabidopsis* (2), *Arabis* (36), *Armoracia* (2), *Athysanus* (1), *Barbarea* (4), *Berteroa* (1), *Brassica* (5), *Braya* (3), *Bunias* (1), *Cakile* (3), *Camelina* (3), *Capsella* (1), *Cardamine* (23), *Cardaria* (3), *Chorispora* (1), *Cochlearia* (3), *Conringia* (1), *Coronopus* (2), *Crambe* (1), *Descurainia* (8), *Diplotaxis* (3), *Draba* (48), *Eruca* (1), *Erucastrum* (1), *Erysimum* (9), *Eutrema* (1), *Halimolobos* (3), *Hesperis* (1), *Hutchinsia* (1), *Iberis* (2), *Idahoa* (1), *Isatis* (1), *Lepidium* (15), *Lesquerella* (5), *Lobularia* (1), *Lunaria* (1), *Malcolmia* (1), *Matthiola* (1), *Myagrum* (1), *Nasturtium* (3), *Neslia* (1), *Parrya* (2), *Physaria* (1), *Raphanus* (2), *Rapistrum* (2), *Rorippa* (11), *Schoenocrambe* (1), *Sinapis* (2), *Sisymbrium* (3), *Smelowskia* (7), *Subularia* (1), *Teesdalia* (1), *Thelypodium* (1), *Thlaspi* (2), *Thysanocarpus* (1).

Validation of taxa

The following three taxa included in the Key to the Brassicaceae of Canada and Alaska have not previously been validated:

Descurainia incisa (Engelm. ex A. Gray) Britton var. *viscosa* (Rydb.) G. A. Mulligan, *comb. nov.*, based on *Sophia viscosa* Rydb., Bull. Torrey Bot. Club 29: 238, 1902.

Smelowskia johnsonii G. A. Mulligan, *sp. nov.*: *Smelowskia johnsonii* a certis *Smelowskia* praedites foliis caulinis late oblongis vel ovatis, integris vel minute denticulatis, densissimis pilis simplicibis albis-villosis.

Smelowskia johnsonii differs from other *Smelowskia* by its oblong to ovate, entire or shallowly toothed cauline leaves that are densely covered by long, simple, white-villous trichomes.

Holotype: Hills adjacent to Kukpuk River, Lat. 68°17'N, Long. 165°32'W, Alaska. Elevation 300-1400 ft., steep slopes and ridges of Flint Mountain and surrounding hills. Talus slopes, *A. W. Johnson, L. Viereck and H. Melchior 688*, 15–16 Aug., 1959 (DAO).

David F. Murray, University of Alaska Museum, Fairbanks, said, in a fax dated 18 November 1997, that the Museum also has a specimen of this taxon from the same general area, *Viereck and Bucknell* 4359.

Smelowskia media (Drury & Rollins) G. A. Mulligan, *sp. nov.*, based on *Smelowskia calycina* var. *media* Drury & Rollins, Rhodora 54: 100, 1952. *Smelowskia media* is only known to have the chromosome number of $2n=12$: Alaska, Dawe & Murray (1981); Yukon, *Calder 34286 & 34367*, Department of Agriculture Herbarium, Ottawa (DAO), Mulligan (unpublished).

Species in the genus *Smelowskia* in Canada and Alaska

1. *Smelowskia borealis* (Greene) Drury & Rollins (AK, YT, NT-M). Native.
2a. *Smelowskia calycina* (Stephan ex Willd.) C. A. Mey. var. *americana* (Regel & Herder) Drury & Rollins (AB, BC). Native.
2b. *Smelowskia calycina* var. *porsildii* Drury & Rollins (AK). Native.
3. *Smelowskia johnsonii* G. A. Mulligan (AK, Bering Strait). Native.
4. *Smelowskia media* (Drury & Rollins) G. A. Mulligan (AK, YT, NT-M). Native.
5. *Smelowskia ovalis* M. E. Jones (BC). Native.
6. *Smelowskia pyriformis* Drury & Rollins (AK). Native.

Key to species in the genus *Smelowskia* in Canada and Alaska

1. Caudex mostly branched, slender, stems usually simple, each arising from a separate caudex branch; pedicels divaricate to ascending 2
1. Caudex mostly simple, stout, more than 5 mm in diameter; stems branched from near base upward, becoming decumbent in fruit; pedicels widely divergent to arcuate 6

2. Mature siliques oblong, tapering at both ends; sepals caducous; basal leaf bases strongly ciliate with long acicular trichomes 3
2. Mature siliques ovate to slightly oblong, truncate at base; sepals persistent; basal leaf bases not ciliate ..... *5. S. ovalis*

3. Basal leaves entire or very shallowly toothed at the tips; cauline leaves entire or very shallowly toothed ... 4
3. Basal leaves pinnately lobed; cauline leaves pinnately lobed; caudex leaves broadly oblong to ovate 5

4. Caudex leaves broadly oblong to ovate, densely covered with long, simple, white-villous trichomes ..... *3. S. johnsonii*
4. Caudex leaves linear to narrowly spatulate, densely covered with short dendritic trichomes ..... *2b. S. calycina* var. *porsildii*

5. Pedicels widely divaricate, angle of divergence 50° to 80°; siliques broadest above the middle; cauline leaves few-lobed, 2 or 3 per stem ..... *4. S. media*
5. Pedicels ascending, angle of divergence less than 50°; siliques broadest at the middle and below; cauline leaves many-lobed, 3 to 7 per stem ..... *2a. S. calycina* var. *americana*

6. Basal leaves pinnately cut to the midrib the full length of the blade, *ca* 9-lobed, petals white or cream-coloured; sepals tan, *ca* 1 mm long; siliques elongated, pear-shaped, 5 to 6 mm long, *ca* 2 mm wide ..... *6. S. pyriformis*
6. Basal leaves palmately 3- to 5-lobed, lobes short; petals purple; sepals purple, *ca* 2.5 mm long; siliques broadly ovate to oblong or linear, 5 to 19 mm long, 3 to 6 mm wide ..... *1. S. borealis*

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Trillium ovatum Pursh variety *hibbersonii* (Taylor *et* Szczawinski) Douglas *et* Pojar, variety nova

GEORGE W. DOUGLAS[1] and JIM POJAR[2]

[1]Conservation Data Centre, British Columbia Ministry of Environment, Lands, and Parks, Resource Inventory Branch, Wildlife Inventory Section, P.O. Box 9344 Station Provincial Government, Victoria, British Columbia V8W 9M1 Canada
[2]British Columbia Forest Service, Postal Bag 5000, Smithers, British Columbia V0J 2N0 Canada

Douglas, George W., and Jim Pojar. 2001. Dwarf Trillium, *Trillium ovatum* Pursh variety *hibbersonii* (Taylor *et* Szczawinski) Douglas *et* Pojar, variety nova. Canadian Field-Naturalist 115(2): 343.

A new combination, *Trillium ovatum* Pursh var. *hibbersonii* (Taylor *et* Szczawinski) Douglas *et* Pojar, is made within the species *Trillium ovatum* in order to more accurately reflect current taxonomic opinion and provide a more readily traced name in connection with research and conservation work.

Key Words. Dwarf Trillium, *Trillium ovatum* variety *hibbersonii*, new combination, British Columbia.

The Dwarf Trillium, found in British Columbia, has long been of interest to avid rock gardeners and was formally named *Trillium ovatum* Pursh forma *hibbersonii* Taylor & Szczawinski by Taylor and Szczawinski (1974). It is now apparent that this taxon is best treated at the varietal level since it differs from the var. *ovatum* in its consistently shorter stature (which it maintains in the garden), its initial flower color (pink versus white) and its restriction to moist mossy cliffs and river boulders on western Vancouver Island.

Production of the *Illustrated Flora of British Columbia* (Douglas et al. 2001) requires a new combination for this taxon at the varietal level because the flora does not recognize *forma* or trivial variations of plants. This change of rank will more accurately reflect current taxonomic opinion and provide a more readily traced name in connection with research and conservation work. The new combination is documented below:

Trillium ovatum Pursh variety *hibbersonii* (Taylor *et* Szczawinski) Douglas *et* Pojar, variety nova. Basionym: *Trillium ovatum* Pursh *forma hibbersonii* Taylor *et* Szczawinski. Syesis 7: 250. 1974.

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Taylor, T. M. C., and **A. F. Szczawinski.** 1974. *Trillium ovatum* Pursh *forma hibbersonii* Taylor *et* Szczawinski. Syesis 7: 250.

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Killing of a Bison, *Bison bison,* Calf by a Wolf, *Canis lupus,* and Four Coyotes, *Canis latrans,* in Yellowstone National Park

DOUGLAS W. SMITH[1], KERRY M. MURPHY[1], and STAN MONGER[2]

[1]Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, Wyoming 82190 USA
[2]Gallatin Flying Service, Bozeman, Montana 59715 USA

Smith, Douglas W., Kerry M. Murphy, and Stan Monger. 2001. Killing of a Bison, *Bison bison*, calf by a Wolf, *Canis lupus*, and four Coyotes, *Canis latrans*, in Yellowstone National Park. Canadian Field-Naturalist. 115(2): 343–345.

We describe a fatal attack on a Bison calf (*Bison bison*) in Yellowstone National Park by a Wolf (*Canis lupus*) and four Coyotes (*Canis latrans*). A lone adult Wolf bit the neck of a lone, malnourished Bison calf while four Coyotes, simultaneously bit at the hindquarters. After the calf died, the Wolf was intolerant of Coyote proximity to the dead calf, and did not allow the Coyotes to feed or approach the carcass.

Key Words: Wolf, *Canis lupus*, Bison, *Bison bison*, Coyote, *Canis latrans*, predation

Observations of Wolves (*Canis lupus*) killing Bison (*Bison bison*) until now have been limited to Wood Buffalo National Park, Canada (Carbyn and Trottier 1987, 1988; Carbyn et al. 1993) and are fair-

ly uncommon. Most Wolf-Bison interactions involve more than one Wolf (e.g., a pack of Wolves pursuing Bison) and do not involve other carnivores (interspecific cooperation). Bison may be the largest and most difficult prey for Wolves to kill (Mech 1970; Carbyn et al. 1993), so accounts of a single Wolf attacking a Bison are of interest. Of equal interest is when multiple predator species cooperate in making kills. In this case, one Wolf and four Coyotes (*Canis latrans*) simultaneously attacked a Bison calf. Wolves and Coyotes typically do not cooperatively hunt (Mech 1966; Paquet 1992), and Wolves have consistently killed Coyotes since Wolves were reintroduced to Yellowstone National Park (YNP) in 1995 (Crabtree and Sheldon 1999; YNP unpublished data).

Wolf-Bison interactions are becoming more common in YNP as Wolves learn how to prey on Bison (Smith et al. 2000). Wolves have focused their attacks on weak Bison in late winter (Smith et al. 2000), but the observation reported on here is the only interaction where one Wolf was involved, and where Coyotes attacked the same Bison with a Wolf.

The kill took place at Gibbon Meadows, west-central YNP, on 24 March 1999. Weather conditions there are characteristically harsh with long winters (~ 5 – 6 months) and deep snow (90 – 150 cm), even during average winters. Gibbon Meadows is large, approximately 100 ha, and surrounded by Lodgepole Pine (*Pinus contorta*) forests and provides habitat for wintering Bison and Elk (*Cervus elaphus*). Because forage is typically limited in winter due to snow, Bison are often weakened by March or April (Smith et al. 2000). Winter and early-spring losses of Bison to malnutrition are common, numbering 2 to 10 per winter (depending on winter severity) in the meadows out of a wintering population of about 40–80 Bison.

We made our observation while counting Bison from a Supercub airplane 160–170 m above ground. At 0800, we observed a Wolf and four Coyotes attacking a Bison calf. Based on its size the Wolf was >1 year old and likely less than 3 years old, because it was progeny of Wolves reintroduced to YNP in 1995 and 1996 (Bangs and Fritts 1996; Phillips and Smith 1996; Bangs et al. 1999). The four Coyotes appeared to be adults based on their size, but could have been yearlings.

When we first saw the interaction, the Bison calf was prone with its head up and the Wolf was biting the underside of its neck, while the four Coyotes simultaneously were biting the hindquarters. We assumed the bites to the neck were fatal, as we could see no damage from the bites to the rear. This first Supercub left the area, but contacted by radio another Supercub that was aerially tracking wolves and which arrived on the scene 30 min later.

The second Supercub observed the Wolf feeding on the Bison calf, now dead, with four Coyotes bedded approximately 60 – 70 m away. The Wolf remained alone at the carcass while we circled for five minutes after which we departed.

Although the calf was first observed down, we believe it was brought down by the Wolf, and not attacked while prone. We have observed other situations in YNP with malnourished Bison calves, and they stand until almost dead and often survive for prolonged periods in poor condition (Smith et al. 2000). We do not know if the calf was abandoned by its mother, but at the time of the kill the meadow was the only snow-free area and other Bison were nearby.

This is the first reported observation of a Wolf and Coyotes simultaneously attacking prey. However, we doubt that the two species of canids were foraging cooperatively. When Wolves and Coyotes interact in YNP, Wolves usually chase and often kill Coyotes (Allen 1979; Crabtree and Sheldon 1999). Several incidents in YNP have been observed where several Coyotes have harassed and chased away lone Wolves, but this has never been observed at a carcass. The food incentive may have caused the Wolf to defend the carcass more vigorously, but we do not know how long the Wolf was able successfully to control the carcass.

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Short-eared Owl, *Asio flammeus*, Attack on a Burrowing Owl, *Athene cunicularia*, in Suffield National Wildlife Area, Alberta

SARAH D. CARNEGIE, ERIN J. URTON, and DAVID L. GUMMER[1]

Biology Department, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada
[1]Corresponding author, present address: Mammalogy Program, Provincial Museum of Alberta, 12845 - 102 Avenue, Edmonton Alberta T5N 0M6, Canada

Carnegie, Sarah D., Erin J. Urton, and David L. Gummer. 2001. Short-eared Owl, *Asio flammeus*, attack on a Burrowing Owl, *Athene cunicularia*, in Suffield National Wildlife Area, Alberta. Canadian Field-Naturalist 115(2): 345–346.

During nighttime surveys for Ord's Kangaroo Rats in Suffield National Wildlife Area, Alberta, we observed a Short-eared Owl attacking a Burrowing Owl. The incident is of interest because aggressive interactions between these two species have apparently never been documented and because both species are considered at risk by the Committee On the Status of Endangered Wildlife In Canada. Presumably, aggression between these two species is rare; however, such interactions may play a more important role than previously realized in governing the owls' territories and survival, especially in areas of high owl and/or prey densities.

Key Words: Burrowing Owl, *Athene cunicularia*, Short-eared Owl, *Asio flammeus*, attack, attempted predation, aggression, interaction, territoriality, Alberta.

Incidental to our field studies of Ord's Kangaroo Rats (*Dipodomys ordii*) in southeastern Alberta, we recorded observations of Great Horned Owls (*Bubo virginianus*), Snowy Owls (*Nyctea scandiaca*), Burrowing Owls (*Athene cunicularia*), Long-eared Owls (*Asio otus*), and Short-eared Owls (*A. flammeus*). This note recounts an aggressive interaction that we observed between a Short-eared Owl and a Burrowing Owl on 21 June 1999.

We conducted nighttime surveys for Ord's Kangaroo Rats in Suffield National Wildlife Area (SNWA; 50° 35' N, 110° 25' W) on 45 nights during May and June 1999. SNWA occupies 460 km^2 in the eastern part of Canadian Forces Base Suffield, Alberta. Eolian sand dunes, stabilized by native grassland and prairie scrub vegetation, are the most conspicuous landforms in SNWA. Our surveys consisted of field personnel driving a vehicle (< 25 $km \cdot h^{-1}$) along gravel roads, trails, and sandy firebreaks, or hiking on open sand dunes, with spotlights (10^6 candlepower, Brinkmann Corporation, Dallas, Texas) aimed at the edges of vegetation (Kaufman and Kaufman 1982; Gummer et al. 1997; Ralls and Eberhardt 1997).

On 21 June 1999, we conducted a spotlight survey along a 15 m wide fireguard in SNWA. At 00:43, we crested a small hill and noticed a Short-eared Owl in the process of attacking a Burrowing Owl on the ground in the centre of the fireguard. Using its talons, the Short-eared Owl had the Burrowing Owl pinned to the ground. The Burrowing Owl was on its back with its wings spread open and its talons raised in a defensive posture. We approached in our truck to a distance of approximately 5 m from the owls. The Short-eared Owl turned and looked at us but remained atop the Burrowing Owl until 00:48. The Short-eared Owl then fled the scene temporarily. The Burrowing Owl, its movements clearly hindered by its injuries, fluttered across the fireguard to the east bank. The Short-eared Owl suddenly returned (00:49) and resumed the attack briefly before departing. The Burrowing Owl then dropped down from the bank (1 m elevation) onto the road. Its wings were outstretched and twisted and its right eye appeared to be injured. At 00:51 the wounded Burrowing Owl retreated into an abandoned Badger (*Taxidea taxus*) den that was 2 m away.

According to Earhart and Johnson (1970), Short-eared Owls are approximately twice the mass of Burrowing Owls (315 g versus 146 g, respectively). Hence it is not surprising that the larger owl dominated the smaller owl. We do not know if the Burrowing Owl eventually died of its injuries, or if it would have been killed had we not interrupted the attack. We speculate that the interaction may have related to: (i) an attempted predation by the Short-eared Owl on the Burrowing Owl; (ii) conflict over a potential prey item in the vicinity; or (iii) a territorial dispute.

Short-eared Owls are not documented as predators of Burrowing Owls (Haug et al. 1993) whereas Cooper's Hawks (*Accipiter cooperii*), Swainson's Hawks (*Buteo swainsoni*), Red-tailed Hawks (*B. jamaicensis*), Ferruginous Hawks (*B. regalis*), Merlins (*Falco columbarius*), Peregrine Falcons (*F. peregrinus*), Prairie Falcons (*F. mexicanus*), Great Horned Owls, and American Crows (*Corvus brachyrhynchos*) and are all known threats to Burrowing Owls (Wedgewood 1978*; Konrad and Gilmer 1984; Haug et al. 1993). Short-eared Owls are not known to kill any other raptors (Holt and Leasure 1993).

Both Short-eared Owls and Burrowing Owls are considered at risk by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC 2000*). Because of long-term declines in population estimates, Short-eared Owls are listed as "special concern" (Cadman and Page 1994*; COSEWIC 2000*) and Burrowing Owls are classed as "endangered" (Wedgewood 1978*; Haug and Didiuk 1991*; Wellicome and Haug 1995*; COSEWIC 2000*). Aggression between these owl species is probably rare, although it may be more common in areas of unusually high densities of owls and/or prey (e.g., Ord's Kangaroo Rats in SNWA). Interspecific aggression may play a more important role than previously realized in determining these owls' territories and survival. Novel interactions among owls may also become more common as patches of natural habitat and abundant prey decline in frequency and size. Thus, interaction between owls may be yet another factor to consider for conservation and management of Short-eared Owls and Burrowing Owls.

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Arboreal Courtship Behaviour by Eastern Garter Snakes, *Thamnophis sirtalis sirtalis*, in September in Bruce County, Ontario

DAVID A. GALBRAITH

Science Department, Royal Botanical Gardens, P.O. Box 399, Hamilton, Ontario L8N 3H8 Canada

Galbraith, David A. 2001. Arboreal courtship behaviour by Eastern Garter Snakes, *Thamnophis sirtalis sirtalis*, in September in Bruce County, Ontario. Canadian Field-Naturalist 115(2): 347–348.

Courtship behaviour involving an adult female and two male Eastern Garter Snakes (*Thamnophis s. sirtalis*) was observed near Lake Huron in Bruce County, Ontario, in September 1997. Courtship behaviour took place with all three animals located among the branches of a small Jack Pine (*Pinus banksiana*) about 1 m above ground level. Instances of arboreal courtship in Eastern Garter Snakes appear to be most frequent in late summer or early fall in Ontario, and may be related to thermoregulation through direct insolation.

Key Words: Eastern Garter Snake, *Thamnophis sirtalis sirtalis*, arboreal, fall, courtship behaviour, Ontario, Canada.

I observed Eastern Garter Snakes (*Thamnophis sirtalis sirtalis*) on private land in a cottage community on the coastal sand dune area of the eastern shore of Lake Huron (81°44′ W, 44°06′ N), approximately 10 km south-west of the town of Kincardine, Bruce County, Ontario. The area has been developed gradually over the past 40 years from open sand dunes with some native poplars to its present mix of native and introduced trees, bushes and other plants. Eastern Garter Snakes have been seen on occasion in the immediate area in previous years.

Three snakes were observed in courtship in a small Jack Pine *(Pinus banksiana*) approximately 1 m from ground level, beginning at 09:15 h, 14 September 1997 (all times reported are local, DST). The snakes were lying in a fairly exposed position on the eastern side of the tree, approximately 3 m from the front porch of a cottage. Although sunrise occurred at 07:05 h on 14 September 1997 at this location (United States Naval Observatory 1997), the proximity of the cottage kept the snakes' location in shade until approximately 10:20 h. Air temperature on the shaded side of the cottage was approximately 17°C at 09:15 h. Observations were made from (a) behind a bush approximately 2 m from the snakes, and (b) from a garden bench approximately 4 m from the subjects.

I began recording observations and taking photographs at 09:22 h. I designated the snakes as F (female), M1 (male proximate to F) and M2 (male distant from F). When discovered, M1 was on F and M2 was about 20-25 cm distant. M1 appeared smaller than M2. The abdomen of F had a very flaccid appearance, and I conjecture that she had recently given birth. The female F appeared to be particularly large (estimated snout-vent length 700 mm).

Between 09:22 h and 11:00 h the snakes moved very little. M1 actually moved off twice, circling through the branches of the Jack Pine, to return to rest in contact with the female. Sunlight began to hit the males at 10:20 h, and the female by 10:40 h, but remained occasional because of broken cloud cover. By 10:52 h, all three snakes were in continuous sunlight. At 11:00 h the air temperature had risen to approximately 20°C, both males started to move into contact with F, and for the first time probed the air with their tongues. Between 11:09 h and 11:50 h, all three snakes were occasionally in motion. At first, they formed a tight coil, but by 11:32 h looser body coils hung down from the tree. The large female was coiled with her tail and posterior 10 cm of trunk hanging loose. Both males wrapped their tails and lower trunks around the female and appeared to be seeking cloacal apposition, although none was observed (Figure 1).

At 11:50 h, all three snakes moved quickly to ground level. The transition was rapid, and I do not know whether they fell or moved down of their own accord. Once on the ground, contact between the three snakes appeared to continue for approximately five minutes, after which one of the males moved away from the female, while the other remained in contact with her. I caught glimpses of the female for the next few minutes, but she gradually moved deeper under ground cover and I was unable to make further observations. Neither copulation nor direct cloacal apposition were observed. The snakes were not captured following observation.

Snakes in the genus *Thamnophis* most frequently copulate in spring but have occasionally been noted to copulate in the fall, immediately prior to entering hibernacula (Cook 1984). *Thamnophis sirtalis* may mate frequently in the fall, as sperm may overwinter in the oviduct prior to entering the seminal receptacles of the female in early spring (Fox 1956). The possibility of fall mating, followed by sperm storage over winter, has been noted previously in the Red-sided Garter Snake (*Thamnophis sirtalis parietalis*; Crews 1984; Crews et al. 1984; Whittier and Crews, 1986).

FIGURE 1. One female and two male Eastern Garter Snakes (*Thamnophis sirtalis sirtalis*) exhibiting courtship behaviours in a small Jack Pine (*Pinus banksiana*) on 14 September 1997 in Bruce County, Ontario.

Arboreal mating behaviour by *Thamnophis s. sirtalis* was reported in April of 1992 in Massachusetts, when five snakes were discovered in a bird's nest within a Black Willow tree (*Salix nigra*; Martinez 1992). Arboreal courtship and mating behaviour in the Red-sided Garter Snake has been reported in the Interlake Region of Manitoba (Gregory 1975), but in spring.

Unpublished observations of fall courtship or copulatory behaviour and arboreal activity by *Thamnophis s. sirtalis* in Ontario were found in the Ontario Herpetofaunal Summary (OHS) database, made between 1956 and 1994 (M. Oldham, personal communication). Twelve observations of copulatory behaviour were recorded in the database. Two instances of courtship or copulation were observed between August and October, and arboreal activity was reported four times. All four observations of arboreal activity also took place between late August and early October. Twice a single individual rested in a tree or bush, in one instance two snakes were observed together in a tree, and in the fourth instance a male and female were observed mating in a Juniper (*Juniperus communis*) on 14 September, 1992 in the Oakville area of Ontario (unpublished observation of D. Gregory; all OHS unpublished data: M. Oldham personal communication).

From the instance reported here and those in the OHS database, it appears that arboreal activity by *Thamnophis sirtalis sirtalis* may be most common in or around September in Ontario. Arboreal activity may present Garter Snakes with an opportunity to increase body temperature through direct insolation in the cool fall months. Arboreal behaviour also may minimize contact with the ground, which may act as a heat-sink if it is colder than a snake's body temperature. It is also possible that the warming effect of direct sunlight encourages dissemination of olfactory signals important for copulatory behaviour.

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Increases and Expansion of the New Brunswick Breeding Population of Black-legged Kittiwakes, *Rissa tridactyla*

F. PATRICK KEHOE[1, 2] and ANTONY W. DIAMOND[3]

[1]Fish and Wildlife Branch Department of Natural Resources and Energy, P.O. Box 6000, Fredericton, New Brunswick, E3B 5H1 Canada
[2]Present address: Ducks Unlimited Canada, Box 818, Brooks, Alberta T1R 2B7 Canada
[3]Atlantic Cooperative Wildlife Ecology Research Network, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick E3B 6E1 Canada

Kehoe, F. Patrick, and Antony W. Diamond. 2001. Increases and expansion of the New Brunswick breeding population of Black-legged Kittiwakes, *Rissa tridactyla*. Canadian Field-Naturalist. 115(2): 349–350.

The New Brunswick breeding population of Black-legged Kittiwakes has increased to over 100 pairs over the past seven years. There are now colonies at two sites.

Key Words: Black-legged Kittiwake, *Rissa tridactyla*, colony, breeding, New Brunswick.

Black-legged Kittiwakes were reported to breed in New Brunswick among the islands in the Bay of Fundy in the 1800s (Audubon 1840; Chamberlain 1887). However, those early accounts came into question during the species' absence as a breeder in the 1900s (Squires 1952; Palmer 1949). With the discovery of a small colony of 12 nesting pairs on South Wolf Island in the Bay of Fundy (44° 56′N, 66° 44′W) in 1992, Kehoe (1994) documented the first recent records of Black-legged Kittiwakes (hereafter "kittiwake") breeding in New Brunswick.

In 1993, there were 25 nests at South Wolf Island. Since that time the colony has continued to grow, and has supported up to 135 nests. However on 6 July 1996 an exceptional hurricane-induced storm caused the loss of one-third of the nests at this site (K. Mawhinney, unpublished). Kehoe (1994) speculated that Whitehorse Island (44° 59′ N, 66° 52′ W), 12 km north-west of South Wolf, could become a second colony. Kittiwake nests were first found by A.W.D. on Whitehorse on 20 July 1998, and it supported at least 42 nesting pairs and 7 visible downy young on 21–22 July 1999. Some of the 1999 pairs may have relocated from South Wolf Island, as at least that many pairs disappeared from South Wolf some time after 5 May (Table 1).

There is a previous record of 20 pairs of kittiwakes nesting on "Whitehorse Islet" in Lock et al. (1994, Table 5.1). This record is erroneous. Whitehorse Islet is a small flat rock in the Grand Manan archipelago, and lacks the cliff habitat required by kittiwakes; evidently this record confused the locality, as is clear from the coordinates. A. R. Lock (personal communication) confirmed that the record was based on observations by P. Pearce who in turn (personal communication) confirmed that the birds were roosting or prospecting but were not confirmed as breeding, and that the island in question was Whitehorse Island not Whitehorse Islet. Our records therefore are the first confirmation of breeding by kittiwakes on Whitehorse Island.

Kittiwakes have been counted at South Wolf, and Whitehorse checked for their presence, annually since the initial colony was discovered in 1992. We have counted each of these sites independently most summers (Table 1). Both colonies are located on rock cliffs facing south (South Wolf) or southwest (Whtehorse) and nests are located 3–10 m above the high tide line. All surveys have been conducted by boat, from a distance of 15–20 m from the base of the nesting cliff, with one primary observer doing the count. Counts by F. P. K. have been entirely visual; A.W.D. also made visual counts but confirmed them from counts from photographs taken by either himself, K. Mawhinney or F. Huettmann. Nest sites (equivalent to the "occupied sites" of Walsh et al. 1995) were identified by the presence of nesting material (seaweeds and grasses). Ledges that were occupied by a pair of kittiwakes without nest material present were not counted. Breeding was confirmed at each colony by the presence of downy young, but the fate of individual nests was not documented. Variation in counts within years can be explained by differential identification of nests by different primary observers as well as the addition or loss of nests between counts. Counts in May tend to be higher than those in June or July because nest-building begins in May and it is harder to distinguish nests at that time than in July (so roosting birds might be wrongly counted as nesting); A.W.D., who made all the May counts, may also be less conservative than F.P.K. in deciding whether or not a site is occupied by nesting birds.

Since 1992 the breeding population of Kittiwakes in New Brunswick has increased to exceed 100 pairs in most breeding seasons (Table 1). In 1999 the occupation of a second colony by at

TABLE 1. Numbers of Nests of Kittwakes counted at South Wolf and Whitehorse Islands, New Brunswick.

Year	Location	Observer	Date	Nest Count
1992	South Wolf	F.P.K.	8 June	8
	South Wolf	F.P.K.	20 June	12
	Whitehorse	F.P.K.	20 June	0
1993	South Wolf	F.P.K.	10 May	0
	South Wolf	F.P.K.	9 July	25
	Whitehorse	F.P.K.	9 July	0
1994	South Wolf	F.P.K.	8 July	69
	Whitehorse	F.P.K.	8 July	0
1995	South Wolf	F.P.K.	20 June	104
	South Wolf	Mawhinney and Sears 1996	July	132
	Whitehorse	F.P.K.	20 June	0
1996	South Wolf	F.P.K.	22 July	54
	Whitehorse	F.P.K.	22 July	0
1997	South Wolf	A.W.D.	13 May	135
	South Wolf	F.P.K.	9 June	89
	South Wolf	A.W.D.	25 July	92
	Whitehorse	A.W.D.	13 May	0
1998	South Wolf	A.W.D.	6 May	124
	Whitehorse	A.W.D.	20 July	4
1999	South Wolf	A.W.D.	5 May	134
	South Wolf	A.W.D.	22 July	63
	Whitehorse	A.W.D.	5 May	19
	Whitehorse	F.P.K.	21 July	42
	Whitehorse	A.W.D.	22 July	48

least 42 nesting pairs has further secured the re-establishment of this species to its former range in the Bay of Fundy.

Other species of sea birds have also recently re-colonized these and nearby islands. Razorbills have been confirmed as breeding on South Wolf since 1995 (Mawhinney and Sears 1996) and Northern Gannets on Whitehorse in 1999 (Corrigan and Diamond unpublished); both these species had been absent as breeders from these islands since the 1800s.

It is clearly important that the seabird populations at these sites continue to be monitored. Protection from the encroachment of aquaculture and fisheries activity as well as other forms of development and disturbance would likely ensure the continued success of seabirds breeding at these sites. In particular, Whitehorse Island has become a stop for tourist boats that pass close to the colonies, as deep water allows even large boats close access to the base of the cliffs. However such disturbance can result in decreased breeding success through the loss of chicks to predators and inconsistent incubation. Both cliff faces are currently under crown ownership, but have no formal protection.

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A Yellow Wood Lily, *Lilium philadelphicum*, from Nantucket Island, Massachusetts, With Notes on its Occurrence in New England

DENVER W. HOLT[1] and WESLEY N. TIFFNEY[2]

[1]Owl Research Institute, P.O. Box 39, Charlo, Montana 59824 USA
[2]University of Massachusetts, Nantucket Field Station, P.O. Box 756, Polpis Road, Nantucket, Massachusetts 02554 USA

Holt, Denver W., and Wesley N. Tiffney. 2001. A Yellow Wood Lily, *Lilium philadelphicum*, from Nantucket Island, Massachusetts; with notes on its occurrence in New England. Canadian Field-Naturalist 115(2): 351–352.

In July 1985, we discovered a pure yellow flowering morph of the Wood Lily (*Lilium philadelphicum*) L. forma *flaviflorum* Williams, on Nantucket Island, Nantucket County, Massachusetts. This appears to be the first formal report of this color variation on Nantucket Island since 1915, suggesting its rarity.

Key Words: Wood Lily, *Lilium philadelphicum* f. *flaviflorum*, yellow, Nantucket Island, Massachusetts, New England.

On 31 July 1985, we found a Wood Lily (*Lilium philadelphicum*) with a pure yellow, unspotted flower. It was noted between Miacomet Pond and Miacomet Road, near the south-central shore of Nantucket Island, Massachusetts. Nantucket Island (130 km^2) is located in southeastern Massachusetts, and approximately 32 km south of the "elbow" of Cape Cod and 65 km southeast of the New England coast. The island is geologically composed of moraines and out-wash plains derived from Pleistocene glaciation (Woodsworth and Wigglesworth 1934). The island is unique and noted for its composition of maritime heaths or "moorlands" (Tiffney and Eveleigh 1985).

We identified this find as *Lilium philadelphicum* L. forma *flaviflorum* Williams (Williams 1913). The plant grew in a mixed grassy heath and low scrub community. It occurred alongside 72 other Wood Lilies, all sporting the typical orange flower decorated with purple-black spots, characteristic of this species. We returned three days later and photographed the Lily, still in full bloom, but lacking some luster to its color and physical integrity. In 1986, we returned to the site and found only a few typical Wood Lilies and none of the yellow color.

Two color morphs of the Wood Lily have been noted by previous authors on Nantucket. Owen (1888) wrote under *L. philadelphicum* that "A pure orange flower without spots is sometimes found", and Albertson and Hinchman (1921) mention "A yellow form without spots has been occasionally found . . ." in their natural history description of the species. Shurrocks (1958) also mentions the yellow unspotted morph, and probably is referring to Albertson and Hinchman (1921). Neither of these authors elaborated on the number of finds, dates and locations, and this may reflect their unfamiliarity with this morph. The herbarium at the Maria Mitchell Science Center on Nantucket Island, contains one specimen of "*L. philadelphicum* L." collected by U. P. Wehmer on 22 July 1915, from Squam, Nantucket. We could see no spots on this specimen (possibly faded), and on the label was the notation "dandelion yellow".

These are the only records for the Nantucket yellow color morph of the Wood Lily we could find, and all may be referring to the same specimen (Albertson and Hinchman 1921; Shurrocks 1958). No specimens of the yellow morph exist at the New England Botanical Club, Harvard University, Cambridge, Massachusetts or the Gray Herbarium, Warren, New Hampshire. Furthermore, we contacted other field botanists and checked with the Massachusetts Natural Heritage Program data base and could not locate any other records of this morph.

Williams (1913) collected the first specimen of this color morph from East Warren, New Hampshire, and it was believed deposited at the Gray Herbarium. In his review of the literature, he found no other reference to this color morph. Williams did however, receive information from two individuals regarding three observations of this morph. He never saw or received photographs. Other than the original stations cited by Williams (1913) (Warren, New Hampshire; Cape Elizabeth and Bathe, Maine; Marblehead, Massachusetts), we have found no other published records of this yellow morph in New England through 2000.

Although we may have not located all the reports, the yellow morph of *Lilium philadelphicum* f. *flaviflorum* appears to be very rare. Protection of the open heath lands on Nantucket Island where this morph has now been reported twice may ensure its continued existence there. Photographs of the specimen have been deposited at the Maria Mitchell Science Center Herbarium, Vestal Street, Nantucket, and the Massachusetts Natural Heritage Program (MNHP).

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Initial Movements of Juvenile Piping Plovers, *Charadrius melodus*, from Natal Sites in Northwestern North Dakota

JEFFREY M. KNETTER[1], ROBERT K. MURPHY[2], and R. SCOTT LUTZ[1]

[1]Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706, USA
[2]U.S. Fish and Wildlife Service, Des Lacs National Wildlife Refuge Complex, Kenmare, North Dakota 58746, USA

Knetter, Jeffrey M., Robert K. Murphy, and R. Scott Lutz. 2001. Initial movements of juvenile Piping Plovers, *Charadrius melodus*, from natal sites in northwestern North Dakota. Canadian Field-Naturalist 115(2): 352–353.

Post-fledging movements may influence the survival of juvenile Piping Plovers (*Charadrius melodus*) in North America's northern Great Plains. During July 1998, four juvenile plovers fitted with radio-transmitters departed their natal areas, on alkali lakes, in northwestern North Dakota when 24–25 days old. Two of the plovers were not found again. The other two moved about 50 km southeast and south, respectively. They moved again by the following day and could not be relocated. Juvenile Piping Plovers reared on alkali lakes in the northern Great Plains may migrate significant distances from natal areas within only 3-4 days of attaining flight.

Key Words: Piping Plover, *Charadrius melodus*, endangered species, behavior, fledging, migration, radio telemetry, North Dakota, Great Plains.

The Great Plains breeding population of Piping Plovers (*Charadrius melodus*) is listed as threatened in the U.S. and endangered in Canada due mainly to poor recruitment of juveniles into the breeding population (Haig 1985*; Sidle 1985). Behavior and survival of juvenile Piping Plovers have been documented through fledging (21–28 days of age [Prindiville Gaines and Ryan 1988]) but not during post-fledging and migration. Post-fledging survival may be affected by the timing and distance of movements, and by habitats used.

During 1998, we used radio telemetry to monitor movements of juvenile Piping Plovers from natal sites on prairie alkali lakes associated with the Missouri Coteau glacial moraine (Bluemle 1980) in southern Burke and northern Mountrail counties (48°37'N, 102°27'W), northwestern North Dakota. Piping Plovers breed on open, salt-encrusted, gravely shores (Prindiville Gaines and Ryan 1988) of 25 alkali lakes in the area. Adjacent land use is mainly small grain farming, tame hay production, and beef ranching on mixed grass prairie.

We captured juvenile Piping Plovers by hand when they were about 20 days of age and weighed them to the nearest g, using a 100-g spring scale. We attached a 1.0-g radio transmitter (< 2.5% of body weight) to individuals that weighed 40–42 g. Each transmitter (150 MHz BD-2; Holohil Systems Limited, Carp, Ontario) was 15 mm × 7 mm × 4 mm, and had a 10-cm whip antenna. We clipped lower back feathers 1.5–2.5 cm anterior to the uropygial gland, used water-resistant epoxy (Titan Corporation, Linwood, Washington) to attach the transmitter to plastic mesh equal in size to the transmitter base, then attached the transmitter and mesh, with epoxy, to the bird (Warnock and Warnock 1993). Juvenile plovers were released within 15 minutes of capture.

We used a three-element Yagi antenna and scanning receiver (Model R2000, Advanced Telemetry Systems, Incorporated, Isanti, Minnesota) to search for plovers and monitor daily movements from vehicles or on foot. When plovers moved from their natal areas, we searched for them using an airplane (Cessna 170) equipped with a pair of four-element, Yagi antennas (Gilmer et al. 1981). The airplane was flown about 600 m above ground along transects spaced 12–15 km apart. We searched within about 35 km north, east, and west and 180 km south of the last

*See Documents Cited section

known location of an individual bird, focusing the search on potential habitat along the Missouri Coteau and nearby (30–55 km west) Missouri River.

Transmitters were affixed to 15 juvenile Piping Plovers but fell off 11 of these within 24 hours of attachment. Transmitters remained affixed on the other four juvenile plovers through their initial movements from natal areas. These four juveniles were captured on a 34-ha alkali lake on 15 July. On the date of capture, three of the juveniles were 20 days old (determined from records of laying or hatching dates [Murphy et al. 1999]) and the fourth was approximately 20 days old, based on its relative size and plumage development. At this age they could rapidly flap their wings and lift off the ground. They were observed flying short distances (≤ 10 m) 1–3 days later (i.e., when 21–23 days old).

We were unable to detect all four juvenile Piping Plovers, either visually or by telemetry, at their natal lake when they were 25 days old (20 July). Two were relocated on 23 July. One had moved about 50 km southeast to a complex of alkali and freshwater lakes on the Missouri Coteau. The other had moved 50 km directly south to the north shore of a large reservoir of the Missouri River ("Lake Sakakawea"). Neither juvenile could be relocated the following day, despite search via aircraft another 100 km south. The remaining two plovers were not relocated.

Our observations indicate Piping Plover fledglings can depart natal areas on Great Plains alkali lakes within a few days of attaining flight. Furthermore, their initial movements may cover considerable distances. Movements we documented were likely initial migration. They may be corroborated by a record of a colour-banded juvenile plover that migrated more than 2000 km in less than 5 days, from its natal area on an alkali lake in central North Dakota to its wintering range on the Gulf Coast of Texas (M. R. Ryan, unpublished data).

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Evidence of an Indirect Dispersal Pathway for Spotted Knapweed, *Centaurea maculosa*, Seeds, via Deer Mice, *Peromyscus maniculatus*, and Great Horned Owls, *Bubo virginianus*

DEAN E. PEARSON and YVETTE K. ORTEGA

USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, PO Box 8089, Missoula, Montana 59807 USA

Pearson, Dean E., and Yvette K. Ortega. 2001. Evidence of an indirect dispersal pathway for Spotted Knapweed, *Centaurea maculosa*, seeds via Deer Mice, *Peromyscus maniculatus*, and Great Horned Owls, *Bubo virginianus*. Canadian Field-Naturalist 115(2): 354.

Spotted Knapweed (*Centaurea maculosa*) seeds were found in the pellets of Great Horned Owls (*Bubo virginianus*). That apparently resulted from owls preying upon Deer Mice (*Peromyscus maniculatus*) which had incidentally consumed knapweed seeds while foraging for the larvae of biological control agents within knapweed seedheads. Successful germination of 1% of the seeds shows that knapweed seeds recovered from owl pellets can be viable after being ingested by both species and suggest that Great Horned Owls can act as indirect dispersers of Spotted Knapweed seeds.

Key Words: *Centaurea maculosa*, Spotted Knapweed, *Peromyscus maniculatus*, Deer Mouse, Great Horned Owl, *Bubo virginianus*, exotic plants, seed dispersal.

Spotted Knapweed (*Centaurea maculosa*) is an aggressive, exotic plant that has invaded vast areas of grassland and savanna in the western United States and Canada. Spotted Knapweed is known to be dispersed by vehicles, humans, and livestock, but little is known about knapweed dispersal by native fauna. Pearson et al. (2000) documented that Deer Mice (*Peromyscus maniculatus*) incidentally ingested whole knapweed seeds while foraging for the larvae of the gall fly (*Urophora* spp.), biological control agents introduced to suppress knapweed seed production, thereby implicating Deer Mice as potential dispersal agents. However, they did not germinate seeds found in Deer Mouse stomachs.

During April, May, and July 1999, we collected four Great Horned Owl (*Bubo virginianus*) pellets on the Calf Creek Wildlife Management Area about 16 km east of Hamilton, Montana (46°17' N, 114°00' W). The four intact pellets contained remains of at least six Deer Mice, nine voles (*Microtus* species), one shrew (*Sorex* species), and 102 Spotted Knapweed seeds. One of the 102 seeds germinated successfully (1%), and the plant grew to reproductive maturity.

Direct consumption of so many Spotted Knapweed seeds by Great Horned Owls is highly improbable as Great Horned Owls are not known to forage on seeds and no remains of seedheads were found in the pellets. Knapweed seeds found in the owl pellets likely came from the small mammals therein. Of the small mammal species identified within the pellets, only Deer Mice are known to ingest Spotted Knapweed seeds (Pearson 1999; Pearson et al. 2000). Pearson et al. (2000) have shown that Deer Mice incidentally consume whole Spotted Knapweed seeds while foraging for the larvae of the gall flies overwintering within knapweed seedheads. We therefore conclude that Great Horned Owls may function as indirect dispersers of knapweed seeds by preying on Deer Mice that have consumed the seeds. Moreover, because Deer Mice ingest knapweed seeds only incidentally while preying upon the larvae of gall flies, the indirect dispersal of knapweed seeds resulting from this series of ecological interactions is initiated by the very biological control agent introduced to reduce the spread of Spotted Knapweed.

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Cooperative Foraging by Steller Sea Lions, *Eumetopias jubatus*

SCOTT M. GENDE[1], JAMIE N. WOMBLE[2], MARY F. WILLSON[3], and BRIAN H. MARSTON[4]

[1]USDA Forest Service, Pacific Northwest Research Station, 2770 Sherwood Lane Suite 2A, Juneau, Alaska 99801, USA
[2]Institute of Marine Science, 245 O'Neill Building, University of Alaska, Fairbanks, Alaska 99775-7220, USA
[3]5230 Terrace Place, Juneau, Alaska 99801, USA
[4]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518, USA

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Steller Sea Lions were observed cooperatively foraging for Eulachon (*Thaleichthyes pacificus*) and possibly Herring (*Clupea pallasi*) in Berners Bay, southeast Alaska in spring, 1996–1999.

Key Words: Steller Sea Lion, *Eumetopias jubatus*, Eulachon, *Thaleichthyes pacificus,* Herring, cooperative foraging, southeast Alaska.

Predators may forage singly or in groups, and foragers in groups may cooperate when hunting prey. Among the marine mammals, at least five species of whales, both toothed and baleen, are known to forage cooperatively (Clapham 1993; Wursig and Clark 1993; Wells et al. 1999). However, cooperative foraging in pinnipeds has been suspected but not documented. Here we report several observations of 75 to 300 Steller Sea Lions (*Eumetopias jubatus*) foraging cooperatively.

The behavior was observed in late April or early May 1996–1999 during a study of the numerical response of vertebrate predators to the spring spawning run of Eulachon (*Thaleichthys pacificus*), a small anadromous smelt that spawns primarily in mainland glacial rivers from California to Alaska (Hart et al. 1944). Observers were present for a week before the Eulachon entered fresh water and for several weeks during and after the spawning run. Observations were made from a skiff in Berners Bay, a relatively small (4.5 km × 3 km) sheltered saltwater bay, 65 km north of Juneau, Alaska (58°45'N, 135°00'W), that is fed by one clearwater and two glacial rivers.

Around 0800 h on 6 May 1996, SMG and JNW noticed a large disturbance outside the bay approximately 4 km away. The disturbance at first appeared to be the wake of a large boat but within several minutes it became clear that it was a large group of Steller Sea Lions moving synchronously toward the bay. Approximately 20 minutes later, a line of rapidly porpoising Sea Lions was observed moving into the bay toward our skiff. The line of Sea Lions, comprised of about 200 to 300 individuals, was perpendicular to the shore and stretched nearly 0.75 km, with the nearest Sea Lion approximately 0.5 km offshore. Most individuals were no more than a few meters apart. All individuals in the line porpoised for 8 to 20 seconds before diving simultaneously for 4 to 9 minutes, after which the water became calm with no indication that any Sea Lions were in the area. Upon simultaneous reemergence in a different section of the bay, the Sea Lions again porpoised for 6 to 15 s before diving simultaneously. During the third reemergence, the line reappeared in another part of the bay approximately 1 km away. The behavior continued for over an hour, with the foraging "line" moving into and out of different sections of the bay. The number of individuals participating gradually decreased and after 2 hours no more Sea Lions were seen foraging in this manner.

For much of the rest of the day, the Sea Lions formed large "rafts" of 10 to 80 sleeping or resting individuals in the middle of the bay (see also Orr and Poulter 1967). The "line" did not reform that afternoon and we left the area around 1700 h. When we arrived at 0900 h the following morning, the cooperative foraging was already in progress. The line, consisting of approximately 200 individuals, moved throughout the bay for over an hour before breaking apart into large rafts. The behavior was not observed again that spring.

We revisited Berners Bay in the springs of 1997, 1998, and 1999 and similar behavior of cooperative foraging, followed by the formation of large rafts, was observed. On 4 and 5 May, 1997, 100 to 300 Sea Lions participated in the foraging line, and up to 100 Sea Lions were observed cooperatively foraging during the last week of April in 1998. In all years, cooperative foraging was observed only just before, or just after, the first Eulachon entered fresh water.

As a result of the rapid movement and unpredictable location of the foraging line, it was impossible to determine with accuracy the prey species targeted by the Sea Lions while cooperatively foraging. However, in 1996 and 1997 we believe that Sea Lions were foraging on Eulachon for several reasons. First, we were able to observe the rafts at close range and some sleeping individuals had partially consumed Eulachon bodies hanging from their mouths. Second, the cooperative foraging behavior consistently occurred just as the Eulachon run was

beginning. Very little is known about the schooling behavior of Eulachon but anecdotal reports suggest that they overwinter in deep water and, following some environmental cue, rapidly migrate to freshwater spawning areas. Thus, Sea Lions may have been targeting schools of Eulachon as they moved into Berners Bay en route to the rivers where they spawn. Herring (*Clupea pallasi*) may also have been the prey pursued by the Sea Lions while cooperatively foraging. Herring spawned extensively along the eastern shore of Berners Bay in 1996 and small groups of Sea Lions (3 to 5 individuals) were seen on occasion foraging for Herring near the shore. However, Herring did not spawn in Berners Bay in 1997 and 1998, suggesting that Eulachon or some other forage fish may have been the prey species pursued during those years.

Although it is difficult to distinguish adult females and immature males while in the water, animals of both sexes and presumably all age classes were observed in the rafts following the cooperative foraging behavior. Berners Bay is located approximately 18 km from Benjamin Island, where 300 to 600 individuals "haul out" from September–May, although they are absent in the summer months (Alaska Department of Fish and Game, 802 Third St., Juneau, Alaska, unpublished data). The "haul-out" is used by adults and subadults of both sexes, including nursing females (JNW, personal observation). Many of the Benjamin Island Sea Lions probably participated in the cooperative foraging behavior, because the "haul-out" was reported to have few individuals during our observations (E. M. Anderson, personal communication), whereas hundreds of Sea Lions were present there the week prior to our observations.

To our knowledge this is the first recorded observation of Sea Lions foraging in this manner, although cooperative foraging has been suspected. Near Unimak Pass, Alaska, large groups (up to several thousand) of Sea Lions were observed simultaneously leaving rookeries or "haul-outs", swimming out to sea and, when schooling fishes were targeted, feeding in groups of up to 50 individuals before simultaneously returning to land in the late afternoon (Fiscus and Baines 1966). When large schools of fish were absent, group foraging was absent or reduced to a few individuals (Fiscus and Baines 1966). Off the coast of central California, Sea Lion rafts, consisting of up to several hundred individuals, were repeatedly observed to dive synchronously (Orr and Poulter 1967). Other observations have been made of Sea Lions foraging in groups (Loughlin and Nelson 1986; references in Hoover 1988) but no studies have indicated the cooperative foraging tactic that we observed.

Sometimes Sea Lions foraged individually for Eulachon in the rivers and probably in the ocean, and we also observed singletons foraging for Herring. However, we know very little of the specific conditions that favor solitary vs. cooperative foraging by Sea Lions. Cooperative foraging may lead to higher per capita energy intake or reduce the risk of poor foraging success (Packer and Ruttan 1988) when prey are aggregated, but such hypotheses remain to be tested in this system.

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A Tribute to Douglas Barton Osbourne Savile, 1909–2000.

J. Ginns[1] and Stephen Darbyshire[2]

[1]1970 Sutherland Road, Penticton, British Columbia V2A 8T8 Canada
[2]ECORC, Wm Saunders Bldg #49, Central Experimental Farm, Ottawa, Ontario K1A 0C6 Canada

Ginns, J., and Stephen Darbyshire. 2001. A tribute to Douglas Barton Osbourne Savile, 1909–2000. Canadian Field-Naturalist 115(2): 357–364.

D. B. O. Savile, honorary member of the Ottawa Field-Naturalist's Club, died in Ottawa on 1 August, 2000. He is survived by his wife of 61 years Constance (Cole), a daughter Elizabeth, a son Harold, and their families.

Doug was an extraordinary individual with an unusually broad range of interests. He was a botanist, mycologist, plant pathologist, ornithologist, and all-round naturalist. Born in Dublin, Ireland on 19 July 1909, his early childhood was spent in western Kenya. At the age of about six he was sent to England for schooling, which was completed at Weymouth College. He moved to Canada in 1928 to take a course in agriculture and in 1933 received a B.Sc. in Agriculture from Macdonald College, Quebec. It was at Macdonald College that Doug's interests in biology began to emerge. He went on to finish a M. Sc. from McGill University (1934) and a Ph.D. from the University of Michigan (1939) where he studied under the mycologist Professor E. B. Mains. He joined the research division of the Canada Department of Agriculture in 1932 as a student assistant on the Fireblight (a bacterial disease of fruit trees) project at Abbotsford, Quebec. From 1941 to 1945 Doug served in the Aero-Engineering Branch of the Royal Canadian Air Force, where he refined his interests in optics, especially pertaining to binoculars and microscopes. His career was spent in the Plant Research Institute (PRI), latterly reorganized as the Biosystematics Research Institute, Canadian Department of Agriculture, Ottawa. At the time of retirement he had achieved the highest scientific ranking, that of Principal Research Scientist. He was assistant curator of the National Mycological Herbarium (known internationally by its acronym DAOM [Department of Agriculture Ottawa Mycology]) from 1943 to 1953, and curator from 1954 to 1967. Although Doug officially retired in July 1974, he hardly broke stride. Appointed as an Honorary Research Associate, he was at his desk almost daily for years afterward, solving research problems, responding to queries and writing manuscripts. During this productive time he published more than 50 papers.

Doug's botanical contributions were often integrated into his mycological research and can be all too easily overlooked. There are, however, several clearly botanical studies of note. Jim Calder, a botanist in PRI, and Doug began a systematic coverage of the flora of British Columbia in 1953. The 1957 Calder, Savile and Roy Taylor collecting trip to the Queen Charlotte Islands led to the Calder and Taylor book *The flora of the Queen Charlotte Islands*. Doug and Jim Calder published three papers on the taxonomy of the Saxifragaceae, they cooperated on a note on the flora of Chesterfield Inlet, and another on the phylogeny of *Carex* in the light of parasitism by the smut fungi. Doug published detailed descriptions of the splash-cup dispersal mechanisms in *Chrysosplenium* and *Mitella* and was interested in the convergent evolution of splash-cup dispersal mechanisms in both plants and fungi. His northern field trips resulted in papers titled: Additional plant records from Spence Bay, Boothia Isthmus; The botany of Somerset Island, District of Franklin; The botany of the northwestern Queen Elizabeth Islands; General ecology and vascular plants of the Hazen Camp area; and, Microclimate and plant growth at Isachsen and Mould Bay. And his 1972 book *Arctic adaptations in plants* brought together his careful observations from the field trips to the Canadian arctic in 1950, 1958, 1959, 1960, and 1962. It has been termed a classic in arctic biology. Other field trips took Doug to Newfoundland, Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Alberta, and British Columbia.

In 1962 Doug published a handbook intended for amateur and professional botanists (including mycologists) titled *Collection and Care of Botanical Specimens*. Doug's thoroughness and attention to detail made this booklet an extremely useful aid for collectors, as well as curators. In its time the publication was one of the few places where consolidated information could be found on all aspects of the collection and care of botanical specimens. This little book proved so useful and popular that it was revised, translated into French and re-published eleven years later.

Mycologically, Doug worked primarily with the groups of parasitic fungi known as rusts and smuts. His research covered taxonomy, ecology, phylogeny, co-evolution of host plants and their parasites, use of

D. B. O. Savile (right) with R to L: J. Walton Groves, Ruth Macrae, Ibra Conners, Mildred Nobles and Clara Fritz, on a collecting trip to Gatineau Park, Quebec, on 12 August 1943.

parasites to decipher host plant relationships, biogeographic history of Canadian plants, and he was involved in developing the use of rust relationships as a guide to taxonomic relationships and comparative chronology of the various groups of grasses. From 1943 through 1953 Doug co-authored with I. L. Conners the annual reports of the Canadian Plant Disease Survey.

Doug Savile was a consummate naturalist writing papers on many subjects, such as meteorological phenomena, flight capabilities of *Archeopteryx*, flight mechanisms of swifts and hummingbirds, and the function and convergence of biogeography. Doug was an avid bird-watcher and student of bird biology. He published several papers on the occurrence and behavior of birds in various parts of Canada.

In 1980 The Ottawa Field-Naturalists' Club awarded him an honorary membership, but Doug's numerous and significant research contributions to botany and mycology both at the Canadian and international level have also been acknowledged by other scientific and academic organizations . He was elected a Fellow of the Royal Society of Canada (1966); awarded the prestigious George Lawson Medal by the Canadian Botanical Association (1976); received an honorary Doctor of Science degree from McGill University (1978); and elected a Distinguished Mycologist by The Mycological Society of America (1988).

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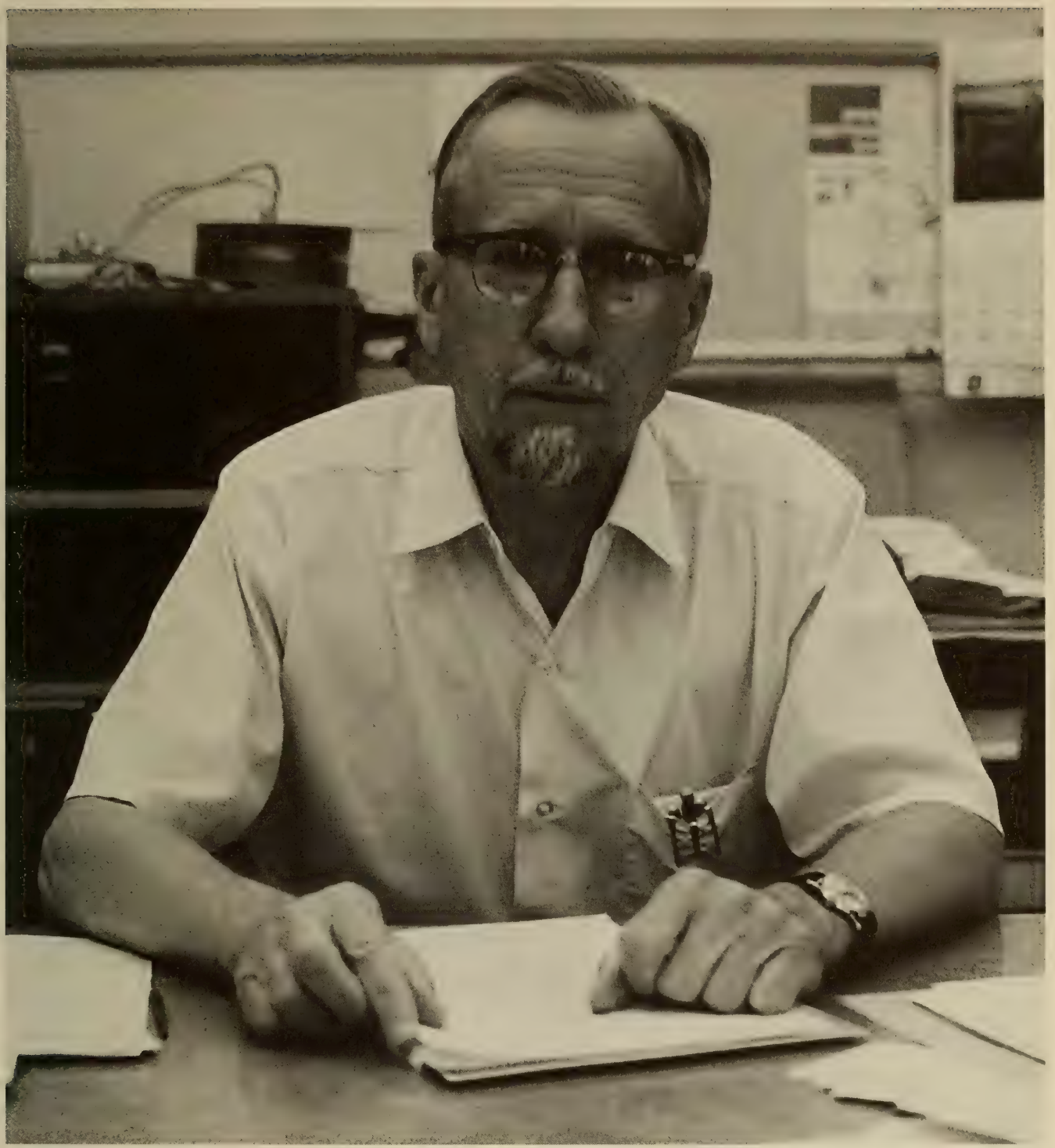

D. B. O. Savile, in 1979 or 1980 at work in the William Saunders Building, Central Experimental Farm, Ottawa. Photo by George P. White.

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Evolution of a Naturalist

D. B. O. Savile†

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For the purpose of this discussion I use the term naturalist for trained biologists who have had ample field experience, at least in the early parts of their careers. Darwin and Wallace were the most important early exemplars of the discipline. Gerald Durrell calls himself an amateur naturalist; but he received substantial professional training in his youth and is really a professional, although he addresses himself to amateurs. The training is usually received, at least in part, in universities; but the committed naturalist pursues knowledge throughout his career. Darwin was trained in university by a reverend gentleman; but what could he have been taught beyond outlines of classification? He took many books with him on the *Beagle* and studied continuously after the voyage was completed. Beatrix Potter was brought up to be a "lady", Victorian style, by parents who abhorred anything smacking of professionalism. She became a competent naturalist by her own endeavours. Among the outstanding biologists, of my acquaintance, Ernst Mayr and Nikolas Tinbergen are proud to be known as naturalists; and I am glad to follow humbly in their footsteps. There are laboratory workers who believe that they alone are biologists. They have my sympathy for their mental myopia.

I suppose that all biologists recall one or more teachers who stimulated their interests and guided them into a career. I met with little such stimulus until I went to university, and consequently was slow in developing serious biological interests.

1. Childhood and school

Spending most of my first six years at Maseno, then a small, isolated settlement on the equator at 1500 m in western Kenya (in those far off days still British East Africa), I had a promising start, as my mother was mildly interested in natural history. I never saw much of the larger animals, except zebras, giraffes, and ostriches, which we saw from the train. (In those days the train ran from Mombasa on the coast only to Kisumu on an arm of Lake Victoria).

When my father went to Maseno, as a missionary and manager of a sisal plantation, the land was largely covered in tall grass, which had to be cut before he could run a survey of the land allotted for development. I suppose the later extensive plantings of maize and sisal may have discouraged a lot of herbivores. Certainly there were carnivores, which we seldom saw; but pet dogs and escaped tame rabbits had a brief existence. My father had to dispose of leopards occasionally, if they turned man-eater. I do remember the hyena. I trotted off one day to meet a visiting relative coming by the trail from Kisumu. Unfortunately, I picked the wrong fork where the trail divided. The guest had arrived before they missed me; and when an adult caught up with me I was standing still, face to face with a hyena. I recall that I was staring solemnly at it, and can only suppose that my steady gaze discomposed it. If I had known enough to be frightened things might have been different. But perhaps I just looked too skinny for it to bother with.

We used to catch chameleons occasionally, trying to make them change colour to match any background. They were also popular as flycatchers. Many of our observations were of insects. I recall mother showing us mantises that closely mimicked a curled up leaf. Very small children can focus down to a few centimeters. When I was perhaps four and my sister close to six, we spent an improving half hour or so watching termites repairing damage to their mud dwelling. Each animal placed its mud pellet in position and then rapped it quite hard with its mandibles. Mother was interested in the story, but, with her adult eyes, naturally could not confirm it. Whether this behaviour was already known I have no idea.

Our attempt at similarly studying safari ants on the march was less successful. We knew enough not to touch the actual column, but thought we could watch from a step or so away. Naturally a scout brought in a company of soldiers to deal with us. My impression was that they bit simultaneously all over me; but perhaps one started and the victim's reaction set all the others biting. We ran screaming to the house,

†Deceased. This personal account of his life was among D. B. O. Savile's papers and well reflects the development of his contributions against the background of people and time he was influenced by. It is complementary to the text and bibliography presented by Ginns and Darbyshire as part of their tribute. It is (except for expanding some abbreviations for clarity) unedited. If Dr. Savile was still living we would have been tempted to negotiate and perhaps soften some of his personal judgements of contemporaries, and eliminate some of the repetition toward the end. Readers should realize that many comments here may be more reflection of a particularly dry sense of humour than purely intemperate judgements. – F. R. Cook

and the household quickly peeled off our clothes. Removing the soldiers is not easy, as the mandibles lock into one's flesh. Pulling often left the head behind and scissors were then used to separate the mandibles, which were pulled out individually. The lesson is that if you must watch the march, stand back about 2 meters — and still watch out for soldiers climbing soft-footedly up you. Today, of course, I would use a pair of field glasses modified to focus down to under two meters (feasible with some center-focusing models).

Returning to England to go to school I received absolutely no stimulus from any teacher in any field of natural history. In high school I did have science teachers, who dealt crudely with the merest fringes of physics and chemistry. One was a motor-cycle enthusiast, from whom I acquired some knowledge of internal combustion engines, to accompany what I learned of steam engines from a model engineering magazine. Throughout my years in England my elder brother and I tried to learn bird identification in summer holidays spent in rural Devon; but, without even a pair of opera glasses between us, we did not achieve very much.

2. Introduction to Agriculture

I moved to Canada in March 1928, to take a two-year course in agriculture at Macdonald College, with summers spent on farms. I travelled, courtesy of the Canadian Pacific Railway Company, who, with the Canadian government, offered assisted passages to potential farmers. The idea was that we would finally buy some of the land held by C.P.R. in Western Canada. It was clear from one summer on a farm that without capital that one could work a life time on farms without getting a down payment on one. However, off I went to a farm at Mystic in extreme southern Quebec, assigned to me by the faculty member at Macdonald who coped with the diploma course students. The farmer, his wife, the hired girl and a permanent hired hand were all supremely ignorant of the world around them. The hired girl did warn me not to touch what she called "poison ivory", but did not even explain that it was a plant. I got a few practical pieces of information from an Irish boy who had been working on a neighbouring farm for a year or two; he at least was vocal.

As the weather warmed up I naturally saw a few animals: woodchucks, the more conspicuous birds and a few snakes. After I had seen my first garter snake, I casually asked if there were any poisonous snakes in Canada — a reasonable question from one reared in the tropics. The response was a mixture of hilarity and indignation. Of course, there were no poisonous snakes in Canada! How could I be so ignorant? Poisonous snakes were tropical!

One day later in the summer the dog and I went along the lane to the back of the farm to fetch the cows. As we crossed the rocky, wooded ridge that divided the cultivated fields a coiled snake raised its head and buzzed at us. Not a very impressive sound, but I could see that the buzz was produced by the tip of the tail. Clearly a rattler! In the days of silent films I could have no idea what a rattler sounded like, but I had imagined something more startling. I grabbed the dog by his collar as he lunged at the snake; then I crippled the snake with a well-directed stone, finished it off with a stick, and hung the corpse on the fence. The rattle was perhaps a centimeter long but with several distinct segments. I was distinctly relieved to have held back the dog, because I would have been held responsible had he been bitten. As junior hired man I was responsible for everything that went wrong on the farm. I did not even mention the incident. In my week or so at Macdonald I had met no biologists, and had not even heard of the National Museum. Consequently I left the snake on the fence and finally forgot about the episode. Many years later, after seeing an article on rattlesnakes, I recalled it and told the story to Clyde Patch. He confirmed that it had to be the Massasauga Rattlesnake, *Sistrurus catenatus*, recorded sparingly in northern New York but not in Quebec*. I realize now that in preagricultural days it must have been more widespread, but clearing the land exterminated it except on rocky ridges.

Returning to Mac, I entered the diploma course and, among others, I took a course on fungal diseases, put on by J. E. Machacek, who was then completing his Ph.D. He was the first teacher who brought a botanical topic to life for me. Already considering transferring to the B.S.A. course, I was persuaded by his lectures to specialize in plant pathology and mycology.

3. Training in Biology

Transferring to the B.S.A. course was not very simple. Like other British students I had entered the diploma course with the understanding that I could take a transition year, followed by the standard third and fourth years. When the schedule was changed, making the first two years standard B.Sc. courses with no agriculture, the transition year had to be abandoned. Four of us protested vehemently and we ended up taking all the courses of the first two years that we could not talk our professors out of agreeing to. I had to skip first year chemistry and math. The chemistry did not matter, but the math showed me

*More likely he meant a Timber Rattlesnake, *Crotalus horridus*, which has occasionally been reported although never verified in Quebec, along the Quebec-New York border (see Claude Melanson 1961. Innconus et Mccones: amphibians and reptiles of Quebec. La Provancher Société, Quebec, Second edition). The Massassauga has never been reported from Québec – F.R. Cook

how shamefully I had been ignored in my last year in school: I did not have the coordinate geometry that leads to the calculus. I survived but it was a gruelling undertaking. Dorothy Newton (later Swales) put on the freshman botany course. She was such a spirited lecturer that I would probably have majored in phanerogamic botany had there been such an option.

In the summer of 1931 I worked for J. G. Coulson in the Plant Pathology Department, and this included the planting and care of field plots. When not needed by him, I helped Dorothy Newton in the then primitive herbarium, mounting specimens that had been 15 years or more in newsprint, and also finding my way about *Gray's Manual*, edition 7, in hopefully identifying many specimens.

In the third year I took elementary genetics, a technique course that covered cytological methods, and a comparative morphology course that included substantial cytology of the major plant groups. Thus I had a foundation for a field that I then had no idea of entering. I also had a half year of mycology and a full year of plant pathology.

4. Fire Blight and the Division of Botany

In the spring of 1932 I applied for a position in the fire blight investigation at Abbotsford, Quebec, having heard that a second appointment was planned. As it happened they were considering appointing an entomology student, but no appointment was made that year. However, the Division of Botany at Ottawa now had my name. Thus, when the incumbent was killed in a car accident, I was phoned by H. N. Racicot to get ready to leave, and he picked me up later in the day (a Saturday). So I was hastily indoctrinated into the experimental work and the operation of a weather station. We had to go to church next morning, to a memorial service for my predecessor. The plate came round, so all I could do was to put in the only money that I possessed, a 50-cent piece, which I had earned by inking diagrams for a graduate student's thesis. So before Racicot returned to Ottawa I had to touch him for an advance. We were then in the depression and living on credit was normal.

There was little spare time that summer, as the copying of the weather records was far behind schedule; and, because bacterial diseases were covered in the final year, I had to read up all that I could find on fire blight. Fortunately the pollination of the trees in insect-proof cages had already been done. I was able to buy an ancient bicycle, which I christened the Death Rattle: no bell was needed, for everyone could hear it coming. The chain kept coming off, owing to having been bent. It was not a standard chain, but luckily I found its mate in Eaton's catalogue and replaced it. I could then travel at 10 m.p.h. without mishap. Our plots were mainly in orchards 2 miles in one direction and 3 miles in the other from the home base. On a state visit next year, Dr. Güssow disapproved of my bicycle (a much better one and fitted with a box for carrying Petri dishes, etc.) and said I should buy a car to save the government's time. I replied that I should be glad to do so if given a salary that permitted it. I remained a cyclist. My pay worked out at about $90/mo., based on a 60-hour week. Fortunately, I paid no rent and did my own cooking; and thus I saved substantially toward the next winter's costs.

Being alone that first summer I put in a full 6-day week, well over 10 hours per day, and still had to tend the weather station on Sunday. However, browsing around on Sunday I used to collect a few plants, which I hopefully identified with an acquired copy of *Gray's Manual* or *Bailey's Manual of Cultivated Plants*. Thus I gradually learned many plants of what I later realized to be an attenuated Appalachian flora. (Some plants I did not see again until attending meetings in Massachusetts about 30 years later). What provoked my interest in learning to recognize plants? Surely Dorothy Newton-Swales' stimulus was important; but I recall insisting that if I was to collect and study parasitic fungi I had to learn their host plants. Accordingly, I collected very few fungi during my first two or three summers at Abbotsford. As soon as Arthur's *Manual of the Rusts* appeared in 1934 I bought a copy, and from then on the rusts were my main concern; but I continued to collect other foliicolous fungi as time permitted.

In the summer of 1933 I must have identified a good many plants, although, like most beginners, I was still avoiding the grasses and sedges. My final undergraduate year (1932–33) included systematic botany, under Dorothy Swales, in which I was ahead of the class, partly because I was familiar with the use of keys and partly because I could recognize many genera. I vaguely recollect that in the two exams I received the highest marks ever given for the course. In 1935 Fr. Marie-Victorin commended me for disentangling the dwarf *Euphorbia* spp., including *E. glyptosperma*, which was not in *Flore Laurentienne*.

In the fall of 1933 I registered for my M.Sc. under Prof. J. G. Coulson. Because of my experience with fire blight, Coulson suggested that I study the limiting factors in some bacterial leaf spots, paralleling a recent study on some fungal leaf spots. Some of the observations seemed interesting, and Coulson suggested that I present them at the spring meeting of the Quebec Society for the Protection of Plants. I gave the talk and, at his request, turned the final manuscript over to Coulson who was to deliver it to the editor. In due course the proceedings appeared and my paper was not included. Surprise, surprise! Coulson had failed to transmit the manuscript. This was my first experience with a non-publisher and,

coupled with later experiences in Ottawa, it could have been disastrous. I wonder if supervisors (well, *nominal* supervisors anyway) appreciate how much their dilatoriness (or worse) may damage a student's career. How can a student expect a fellowship if he has nothing to show that he can do research?

I barely got my thesis turned in by the deadline for fall convocation. Each edition was pronounced perfect by J.G.C.; then, after it was typed, he would want it all changed. I think there were five editions. Once I got the phone call on Friday even after my fellow-student had gone off for the weekend; and I could not move until Monday as someone had to maintain the weather station. I was to have gone to Ottawa for the winter but was fired by telegram at the last moment (H. T. Güssow having evidently cleaned out the money for one of his royal tours). After convocation I accordingly caught a boat to England for a family visit. Thus the winter was essentially wasted.

The fire blight work continued in the spring of 1935 fairly satisfactorily, except that when I wrote up a report on any aspect of the work it quietly disappeared. I continued with all of the work as originally planned and new aspects as they occurred to me, most of which I cannot now recall. (Yes, despite statements to the contrary, ants were up the apple trees throughout the day and night in fine weather, dodging clearly exuding cankers, but surely carrying some bacteria. I checked one tree group hourly for 72 hours until I crossed the tent to turn off the alarm without waking!) Of course all the notes and drafts went home with Homer Racicot and were never heard of again.

The fall of 1935 was an echo of 1934. I was packed and ready to go to Ottawa in the lab car when I was again fired by telegram (N.S.F.; perhaps another royal tour). Stopping at Macdonald I found that Harold Brodie had come on staff. I had already met him and was impressed especially by his productivity — he had already published several papers. I found a small grant available to add to my $300 summer savings, and registered again in graduate school. I took advanced mycology from him and made a good start in rust cytology, using several differential staining techniques, some of my own devising. Brodie and I were soon firm friends. On the first weekend I walked back to the college woods to look for rusts and to botanize generally; and promptly met the Brodies (Helen wearing a shocking old hat of Harold's to keep the flies off) collecting agarics for class use. As naturalists we spoke the same language. Before winter's end he realized that my interest in the rusts was serious and encouraged me to try to get to Ann Arbor and take my doctorate under E. B. Mains.

In the spring of 1936 I returned to Abbotsford for the last season; really a waste, when I look back on it, as all my writeups kept disappearing, "taken home to read over the weekend." A couple of years later when I read Don Marquis' *Archie and Mehitabel*, I recognized Homer's prototype: Freddie the Rat, another inhabitant of Don Marquis' office, was a literary critic. He would read one of Archie's poems, sniff, and then eat it. Homer Racicot to the life!

Soon after I reached Ottawa, Dr. Güssow, sick of the lack of results from the La Pocatière Lab on what was then known as bacterial wilt and rot of potatoes, dumped the problem on Racicot and me, which in effect meant me. The "bacterial" in the common name was a lucky guess, for all that previous investigation had isolated were yellow saprophytic bacteria and soil yeasts. During the preceding year at Macdonald I had told J. C. Perrault that, if he would fix infected tissue, I would embed, section and stain it. That would have given the answer, for one of my stock methods for showing pathogens in plant tissue was Gram staining with a counterstain; but he declined the offer. When I received material for study I at once started pouring dilution plates, but simultaneously fixed and embedded stem and tuber tissue material. As it happened I first got the pathogen from plates, slightly speeded up by colonies appearing near an actinomycete colony. Obviously it was a slow grower and everyone had thrown out plates after 5 days as sterile. Adding yeast extract to the medium shortened the incubation period. Critics belittled the finding as sheer luck; but a few days after the initial isolation I had stained sections showing the typical Gram positive short rods of what is now recognized as *Corynebacterium sepedonicum*. With Gram positive plant pathogens so rare, its identification took a matter of minutes: bacterial ring rot, known for years in Europe, where small whole potatoes are planted, but causing little damage. In North America, where cut sets are planted (to reduce virus infection), it became extremely serious, for the cutting knife proved to be a more reliable means of inoculation than any that I could devise. I had to take a week's leave and go to Macdonald, at my own expense, to confirm the identification, using differential media in the Bacteriology Department and controlled temperature chambers in the Plant Pathology Department. (I never understood why such facilities were not available in the Bacteriology Division at the C.E.F. How can one study bacteria without them?). I asked Racicot to check symptom development on my inoculated plants in the greenhouse, but he never did so.

Getting priority on this identification was critical, as pathologists in Maine were known to be working on the disease. Accordingly, I wrote up a short paper describing the disease, the pathogen, the main methods of spread, and a Gram smear technique that I had devised for rapid confirmation of the disease. The paper was reviewed by I. L. Conners and F. L. Drayton and was ready for submission to *Scientific*

Agriculture (long since defunct) when Homer roused from his winter dream world long enough to see what was happening. He immediately insisted that he had to be senior author. As he had done nothing all winter except for hindering my work, I said that he had no claim even to be junior author, all my work being done in spite of him. He whiffled off downstairs to Dr. Güssow, who must have had a pretty good notion of the truth, which had been a main topic of conversation in the building for many weeks. He finally came back and said I could be senior author, which I had to agree. After I went to Ann Arbor he, with some additions by I. L. Conners, paraphrased the original paper for *American Potato Journal*, with me as second author. This may have been what persuaded him in later years that all the work had been his.

6. Ann Arbor Days

This key paper fortunately appeared promptly and persuaded the Botany faculty at University of Michigan that I *could* do research. Consequently they yielded to Harold Brodie's urging and offered me a small fellowship. I thus was able to spend two winters at Ann Arbor and secured my Ph.D. in the spring of 1939 under E. B. Mains. My thesis on nuclear structure and behaviour in rusts, successfully disentangled several gross misinterpretations that resulted largely from complete reliance on iron alum hematoxylin staining, which is seriously non-selective. For example, strange figures in mycelium, purporting to be the telophase of one nucleus with a large nucleolus at each end, were shown by Feulgen staining to be four nuclei following simultaneous division of a dikaryon. The "nucleoli" are strongly DNA positive; and the "telophase" is two recently regenerated nuclei squeezing past each other to restore compatible pairing. World War II started just before my paper appeared in *American Journal of Botany* for October 1939. Such esoteric pursuits as rust cytology had to be set aside; J. H. Craigie seems to have forgotten these and other findings when he optimistically turned to rust cytology after his retirement in 1952. He failed to use modern methods and in 1959 published many of the same fictional interpretations commonly made prior to 1939.

I must emphasize that rust cytology is not a topic that can be studied at odd times, especially late in life. I made good progress in the winter of 1935–36, and again in my time at Ann Arbor (1937–38 and 1938–39). Although I used a microscope at Ottawa in 1938 for many hours, mainly checking smears for ring rot bacteria, I received a shock on returning to Ann Arbor after four months absence from cytological study: All the objects in my rust sections seemed extremely small and I could not distinguish fine details. Checking with a stage micrometer assured me that the microscope was undamaged. The trouble had to be in my eyes. To have your eyes fail you half way through a cytological thesis problem is a horrifying thought. I dared not tell anyone but persevered. Sometimes resolution of details was slightly improved and I began to suspect that the problem was physiological or psychological. After a week there was a definite improvement; but it was nearly three weeks before resolution was fully back to normal. This experience should warn anyone against trying to do anything as visually demanding as rust cytology at odd times.

Only recently, when I read Evelyn Fox Keller's *A Feeling for the Organism* (W. H. Freeman, New York and San Francisco, 1983), did I realize that I was not alone in this grim experience. In 1944 Barbara McClintock was invited to visit Stanford to help with the cytological aspects of George Beadle's work on *Neurospora*. She was delayed in completing arrangements before she could pack her microscope and go by train across the continent; so I judge that she must have been away from microscopic work for several weeks. As the story is told, she was also worried that she might not be able to contribute to the project. She set up her microscope and for three days she could see nothing. Realizing (very wisely, I think) that she had to do something positive, she set out for a walk and finally rested on a shaded bench on the Stanford campus. Then suddenly she was sure that everything was going to be all right, and, indeed, everything *was* all right; and the project was very successful. Her recovery was rapid, perhaps partly reflecting a relatively short absence from her studies. It must also be noted that Dr. McClintock was 42 at the time of her experience, solidly established in cytogenetics and probably well prepared to cope with a psychological problem; whereas I, aged 29 and not established in research, was poorly prepared. Whatever the fundamental cause of such a problem, the experience further emphasizes that fungal cytology is *not* something to be taken up at odd moments, and especially late in life when sustained microscopic study is a severe strain.

In 1949, I had a happier experience of visual adaptation. Various people had insisted that the Chimney Swift, *Chaetura pelagica*, beats its wings alternately, despite this being a palpable impossibility because the body would simply oscillate about its long axis with the wings producing little lift or thrust. However, I rigged up a shutter stroboscope in front of one objective of my binoculars and could often briefly stop the wings of a bird flying toward or away from me. The wings were, of course, always both up or both down. The interesting point is that, after doing these observations daily for some two weeks, I could fully resolve the wing motion without the stroboscope (Auk 67: 499–504, 1950). Visual acuity obviously is not wholly explained by geometric optics.

Ann Arbor was a stimulating place to work at in

those days. The Botany Department was large and the staff had very varied interests and experience. Unfortunately I could take few courses in the time available. I did take a cytology course (with unfortunately nothing new in it); and I took Professor Ehlers' course in agrostology, finally reducing my ignorance of grasses and sedges (but unfortunately this was 20 years before modern concepts of the grass subfamilies began to appear). I should have profited from another year, with time to learn more about bryophytes, marine algae and geology. However, my contacts were many and stimulating. I retain a mental picture of Carl Larue (experimental morphologist) and myself staring in at some shrub with leaf galls that looked like spinulose gooseberries. We speculated as to whether the resemblance was merely random. In those days, before the acceptance of transposable genes and DNA transfer, the idea naturally did not get off the ground.

7. War-time Turmoil

Returning to Ottawa after commencement Connie and I were married in late July, which was some compensation for having to work nominally under Homer Racicot. That fall I helped inspectors in their field inspection of potatoes. Usually ring rot, our main problem other than viruses, was clearly distinct; but in one area abnormal weather caused it and black leg to look nearly identical, and Gram smears had to be used freely. The outbreak of war put pure science out of the picture. I have a blurred recollection of committees for boosting food production and of posters that presumably appeared in village post offices where they may or may not have been read.

All the junior staff had to help in the famous national registration. The one memorable question was "Can you milk a cow?" Farm boys looking for a lucrative job in a munitions plant said "No". City boys hoping for a safe rural job often said "Yes". Presumably some beneficial outbreeding in the population resulted. The enormous mass of forms, which could never have been indexed by available means, was stored in an Ottawa building that collapsed under the weight. There are less tedious ways of destroying a building.

I recall two technical surveys by which people with assorted talents could be reached. The military people, in search of tropic-proofing talent later in the war, could have found me by looking under meteorology, fungi and optical instruments. But they did not know of the registers, and found our Division by blind luck (good luck as it turned out).

During the early part of the war I examined countless decaying fruits and vegetables; but my only research paper was a short one on malformation of potato starch grains due to viral infection reducing the elasticity of the leucoplasts. That one seems to have slipped through while Homer nodded (American Journal of Botany 29: 286–287, 1942). H. H. Bartlett enthusiastically proclaimed that this would become known as the Savile phenomenon; but the war was on and nobody even noticed it!

Foolishly I joined the R.C.A.F., trying to make some use of my appreciable and varied technical knowledge. Too late I appreciated a warning to the effect that as a civilian scientist you can talk to people of any rank, and are often listened to, (as indeed I found much later as a tropic-proofing adviser); but as a junior officer you cannot advise or help anyone of a rank above you. The next 18 months were continuous frustration to anyone with a conscience, leavened only by an improved understanding of machine-shop operations and of low-speed aerodynamics; not that I expected to make use of the latter, but I was still interested in learning. I did also develop a simple device to stop static charge from bunching up paper in the met. office teletype. This delighted the C.N. teletype technician, who presumably got credit for introducing it at other stations in his area. My commanding officer, Elmer F. (no, not Elmer Fudd, who was funnier and probably smarter) took a rabid dislike of me, mainly because when he asked my opinion on some problem involving several variables, I remarked that an intelligent answer required considerable thought. He blew right up with "That's the trouble with you civilians; you always want to stop and think. In military action a snap decision is all you want." This was accompanied by a snap of his fingers, one thing that he was good at. Because I was still hoping for a transfer to Operational Research I had to clamp on my tongue, instead of replying that that seemed to explain why we lose the first three years of a war, until some intelligent amateurs get into the higher ranks. Much later I found that I had been asked for by Operational Research but Elmer had turned down my transfer. Too late he found out that it was I (the brainless thinker) who had solved the teletype problem. (There being one in the main office he had heard about.) Suddenly, with my minor gadget that any schoolboy with an inventive turn of mind might have dreamt up, I was an engineering genius to his simple mind. He was plainly embarrassed because he had pressed for my discharge. Even the most honorable discharge is distressing during war, and the fact that Elmer had guessed wrongly about me was not particularly heartening. Most guessers expect about a fifty percent score; but Elmer's score was surely under ten percent; he was an uncanny wrong guesser. However, I may have been more use back in Agriculture than in Operational Research as it turned out.

I returned to the Division as assistant to Ibra Conners, who, as curator of the mycological herbarium, compiler of the plant disease survey reports, and registrar of commercial fungicides, certainly needed some help. Things as once went more smoothly.

Lyle Drayton, having had to deal considerably with Racicot in my absence, had found that my complaints about his obstructionism were more than justified.

As the odd jobs section, Conners and I received not only fungal disorders, but mite or insect injuries, physiological disorders, algae, cyanobacteria, etc. Thus when an army officer, worried about fungal damage to optical glass, came to the Division he was brought up to us. This really *was* an odd job, as I soon found out. I took over the project as I had some familiarity with optical instruments and their servicing, and knew a good deal about meteorology. (I used to coach the met. observers at Centralia on cloud recognition and even cloud transformation.) Thus instrument damage and its prevention became my problem for the last two years of W.W.II, during which time I devoted ca. 15 hours per 60-hour week to it. (This included time spent at home making tools for stripping or adjusting instruments.) Salaries were frozen during the war; however, people with extra work loads could receive a $300 p.a. war duties supplement; but no-one in our Division did. (After taking such an emotional beating in W.W.I, Dr. Güssow probably did not dare to apply for any.) Thus I ended the war at a salary designated for a new graduate with no graduate training or experience. It soon became clear that identification of the fungi in instruments was academic: Many common and widespread species were involved. (The situation was probably somewhat different for fabrics and insulating materials, handled by G. A. Ledingham in N.R.C.) My approach was to improve sealing and thus keep molds, mites and moisture out of the instruments. As Mole said to Ratty, after he cut his shin, my attitude was "Never mind what done it."

Two models of binoculars being built by Research Enterprises Ltd. (R.E.L.), a crown company, were substantially improved by minor modifications, aimed at preventing moisture penetration through pressure changes induced by fluctuating temperature. A more significant change, which would have cured the problem by matched contour milling of the cover plates and mating ends of the body castings, was violently rejected by the plant superintendent. He was quite content to go on filling the gaps with luting compound, which cracks on shrinking just as it does when you caulk your window frames. Yet even in 1943 contour milling equipment and techniques were available. A rifle scope was a trickier problem. A computer (They were human in those far-off days) decided to recompute the optics, to eliminate most of the residual aberrations; so I had time for action before the instrument went back into production. I completely redesigned the sighting head, to guarantee a positive seal. Six instruments were hand made for trials. The one that I saw was certainly a beauty. However, the war was coming to an end and C. D. Howe, who had organized the company, cancelled all contracts and the company instantly disintegrated. The army group with which I had worked also disappeared through transfers and demobilization. I eventually turned my notes and drawings for the sighting head over to the newly founded Defence Research Board as the logical safe depository. All my tropic-proofing reports had security ratings; and so I had no acknowledgeable publications for the work.

Although my time in W.W. II was not entirely unproductive, most of it did not promote my development as a naturalist. My varied activities did at least deter me from becoming an extreme specialist. A working knowledge of low-speed aerodynamics, acquired during the war, led eventually to a detailed understanding of the adaptive characteristics of bird wings (Evolution 12: 212–224, 1957). But even by 1948 I was thinking increasingly in terms of evolutionary adaptations in birds and, certainly soon afterward, of those of plants and fungi.

8. Biological Exploration of Canada

After the war I was able to spend slightly more time on mycological studies; but, with Lyle Drayton serving full time as Associate Dominion Botanist, I was still stuck with all the work on diseases of ornamentals and plant quarantine interceptions until a position in this field was filled.

At this point, credit must be given to K. W. Neatby, who, as Director of Science Services, strongly encouraged his staff to explore the country. Tragically he died just when the results of his stimulus were starting to show. With the onset of the Northern Insect Survey, with which I served three seasons as a botanist, describing biting fly habitats, I inevitably learned something of the ecology of the plants and their parasites. For example, in 1949, my first full season in the field, I found that at a tree-line site (Great Whale River or Poste de la Baleine) obligately heteroecious rusts occurred only if the alternate hosts were virtually in contact. Thus my studies of rusts and other parasites were increasingly in terms of hosts and host environment. I think that, by the time I joined J. A. Calder for the start of the British Columbia floristic survey in 1953, I qualified as a professional naturalist although I obviously had a lot to learn — especially as neither of us had set foot in the Cordillera.

Working with Jim Calder was an education in itself. Not only was he a meticulous collector, whose specimens were clean, well-folded and well-dried; but he put more ecological data on his labels than was usual at that time. I like to think that I contributed my bit in 1953 when we invaded completely new country without an appropriate flora for reference. I took along an aircraft altimeter, which allowed us to record altitudes accurately. Equally important in mountain country, as we soon came to realize, is the direction of slope: the difference between north and

south exposure may be equivalent to several degrees of latitude. During the previous winter I found that our British Columbia. collections of many plants were devoid of fruit. In case we should not be able to collect fruiting specimens later, we accordingly included old fruiting stems of flowering perennials. Calder's primary training was in geology; and from him I learnt more of physiography and glacial geology than I had worked out for myself in the Hudson Bay region and northernmost Newfoundland. In British Columbia we thought from the start in terms of biogeography and late glacial history. This approach also influenced my mycological work; one example being studies in the co-evolution of Saxifragaceae and their rusts, which developed over many years, terminating in a summary in *Annals of the Missouri Botanical Garden* 62(2): 354–361, 1975.

I worked with Calder in 1953, 1954 and 1957, the last season being spent in the Queen Charlotte Islands. Botanically the Q.C.I. were exciting, demonstrating the occurrence of a low-level refugium on the west coast contiguous to the deep water of the Pacific Ocean. Unhappily I caught a cold on the ship from Vancouver and, in the dank hotel at Queen Charlotte City, never completely threw it off. I was a drag on the party climbing the small, but steep and slippery mountains; and decided that I was too old for such work.

I accordingly was glad to volunteer, on Harold Senn's behalf, to join a party from McGill in 1958 on Somerset Island. I also had a brief arctic field trip before the 1959 Montreal Botanical Congress. In 1960 I worked out of Isachsen on Ellef Ringnes Island, with the Polar Continental Shelf Project. My experience in British Columbia partly prepared me for interpreting what I saw on Somerset and Ellef Ringnes islands. The latter is in the heart of the supposedly ice-free northwestern Queen Elizabeth Islands, pronounced, by those who had never studied them, to be the centre for all Canadian arctic endemic plants. What struck me, as the season developed, was that the flora round Isachsen is very small, the individual plants are very small and sparsely distributed, and, except for *Puccinellia angustata*, which is widespread across the northern islands and Greenland, the endemics are absent. I was able to work out during the summer, from local observations and the known distribution of all the arctic vascular plants, that, although the northwestern islands had intermittently been covered by snow and ice, even since the end of the Hypsithermal Interval, the ice had not been heavy enough to flow appreciably under its own weight. Thus it had wiped out the plants but had preserved rather than erasing small relief features. The fully documented story was presented in *Canadian Journal of Botany* 39: 909–942, 1961. I had clear priority in this crucial discovery, as was fully recognized by arctic workers at Ottawa at that time. (The story was plagiarized a few years later, independently by two other investigators, both of whom had my paper!) It was certainly a breakthrough in our understanding of arctic biology and late glacial to postglacial history, completely reorganizing several concepts.

The extensive collecting by our botanical and mycological staff saw the introduction of various new techniques, including the evolution of the field press, and caused me to write *Collection and Care of Botanical Specimens* Canada Department of Agriculture, 1962, 1973, which went through two English and one French edition, not to mention a pirated Russian edition.

9. Some Fruits of Field Work

In 1962 I spent the summer at Hazen Camp in northern Ellesmere Island, collecting plants and fungi and supplying the ecological background for studies by the entomologists. Fortunately, I was once more in good condition, for in that dry Shangri-la I had to do a good deal of mountain climbing to reach some species. For a high-arctic site Hazen Camp was very rewarding botanically, mycologically and ornithologically — and indeed entomologically as my colleagues demonstrated. With complementary studies by J. A. Parmelee on Axel Heiberg Island in 1961, and at various DEW Line sites in 1963 and 1967, our picture of geographic patterns of vascular plants and parasitic fungi in the Canadian Arctic was reasonably complete. Thus, I had ample data for biogeographic and evolutionary studies of both plants and rusts. For example, I was able to demonstrate clinal variation in *Puccinia cruciferarum*, a microcyclic rust without pycnia (Mycologia 56: 240–248, 1964) exploding the dogma that without pycnia there could be no genetic recombination. The conspicuous distinctions of *Puccinia poae-nemoralis* ssp. *hyparctica*, in spore size, pigmentation, wall thickness, wall sculpturing and host specialization, have all accumulated since the onset of the Wisconsin glaciation, supplying the strongest support for parasexual recombination in the rusts (*Arctic Adaptations in Plants*, page 61, 1972). The incomplete segregation of *Poa hartzii* from *Poa glauca* evidently occurred in the same period.

My booklet *Arctic Adaptations in Plants* (Canada Department of Agriculture Monograph 6, 1972) brought together most of my own and other peoples' observations on plants and fungi. The first printing of 2000 was exhausted in two years. A second printing of 3000 was exhausted by 1974; and a third printing of 3000 is still in occasionally demand. Clearly it filled a need. About half the content was either original or from my own publications. It certainly represented a large return on a few seasons of field study.

Successful evolutionary studies must usually have an interdisciplinary aspect. When H. J. Brodie (Canadian Journal of Botany 29: 224–234, 1951) clarified the splash-cup dispersal mechanism he spoke of raindrops as the active agents; and probably no-one seriously questioned his terminology. However, even then, through my work on fire blight and my reading in meteorology, I knew that rain rarely falls vertically and that the drops are small; but I did not pursue the question. In the summer of 1958 I found *Chrysosplenium rosendahlii* Packer (misnamed by me in Canadian Journal of Botany 37: 999, 1959, as *C. iowense*) growing freely in moist grass and sedge meadows in southern Somerset Island Although rain is not rare in that region, it is usually fine and slanted by wind. Could the large drops falling scarcely half a metre from grass or sedge panicles possibly operate the splash-cups? It seemed unlikely; but I was uneasily aware that drops from a canopy are large, for their sound on an umbrella is much louder than that of raindrops in the open. I searched the meteorological literature for help in vain. (Meteorologists are more concerned with terminal velocities of drops than with their initial acceleration). In 1972, as the publisher's reader of the first draft of *The Bird's Nest Fungi*, I came on Brodie's report of the dry plain around Lima, Peru, where only fog, and no true rain occurs. The fog supports low tussocks of woody vegetation. There, to his astonishment, he found well-developed specimens of the bird's nest fungus *Cyathus olla* on debris under many of the larger and denser tussocks. I was not astonished, but I was exasperated: This was my Somerset Island puzzle in repetition. Again I failed to get any answers to my questions. Years later, when I was again searching in the Agrometeorology library, the director, Dr. W. Baier, asked what my problem was. When I explained he turned me over to Dr. Henry Hayhoe, a mathematician. With published information on terminal velocities of falling drops in a vertical wind tunnel, Dr. Hayhoe was able to derive an equation to give the velocity of a drop of given size at a given distance of fall (Savile and Hayhoe, *Canadian Journal of Botany* 56: 127–128, 1978). Later calculations showed that a 4.5 mm drop (probably close to the minimum size shed from the canopy) after 0.25 m of fall has a much higher relative momentum than a 2.5 mm drop at terminal velocity (Savile, *Davidsonia* 10(4): 65–69, 1979). It must be noted that natural raindrops rarely exceed 2.2 mm diameter, for larger drops break up in a long fall. Had I had mathematical expertise available, this problem might have been solved in 1958.

Not surprisingly, recognition of the mechanism of the splash-cup quickly led to further observations. Brodie demonstrated the springboard dispersal system in *Salvia*, *Ocimum* and *Kalanchoe* (*Canadian Journal of Botany* 33: 156–167, 1955). Independently I recognized it in *Tiarella trifoliata* in the spring of 1953, simply because Calder and I took our first look at the coastal rain forest of British Columbia on a drizzly day. I recorded it casually in a preliminary study of the rusts of Saxifragaceae (*Canadian Journal of Botany* 32: 400–425, 1954) without christening the mechanism.

The misconception by Brodie, following Buller's lead, that these devices are being powered by raindrops became general and even resulted in a comic strip sequence showing *Cyathus* cups (quite well drawn) with peridioles being dispersed, quite impossibly, by strongly slanted raindrops. Until the derivation of Dr. Hayhoe's equation no-one could be convinced that drops from a low canopy could function adequately. Even Brodie, who had a very receptive mind, could not be convinced until he saw the figures in *Canadian Journal of Botany* (1978) and *Davidsonia* (1979). At last he saw how *Cyathus olla* survived in the Peruvian desert (where, I am sure, some rodent emerges in the cool dusk and effects more distant transfer).

Would I have stumbled on the springboard action of the *Tiarella* capsule if I had seen it only on a fine day? Probably not as promptly, but plainly I was thinking about Saxifragaceae in terms of dispersal and was puzzled by the strange capsule of *Tiarella*. I could scarcely have missed it next year in the humid forest east of Prince Rupert where both *T. trifoliata* and *T. unifoliata* flourish.

Looking back after some 35 years, my activities in British Columbia indicate that I was thinking as a naturalist, considering plants and fungi in terms of Pleistocene glaciation, biogeography, means of dispersal, etc., although I had a lot to learn. Well, the active naturalist never stops learning. For example, I was trying to shake off the appallingly artificial lumping of the rusts of Saxifragaceae. But I was still treating at varietal level rusts that, with more abundant material, later proved to be good species that do not intergrade on contact. Thus it is was not until 1973 (*Canadian Journal of Botany* 51: 2347–2370) that I could present a treatment of all these rusts that still seems essentially satisfactory. My revision was still fully morphological but recognized small, but consistent, differences that most authors had ignored. From work on bacterial diseases and rust cytology I was used to oil-immersion microscopy, which was generally avoided by mycologists because cedar oil had to be wiped off the immersion lens promptly. I pioneered using tri-immersion in examining rusts, and other fungi about the end of World War II, using medicinal paraffin until non-drying immersion oils were available. I found I could measure spores more accurately and faster than with the 4 mm objective. With these characters the rusts of *Mitella diphylla* and *Tiarella cordifolia* (*Puccinia heucherae* var. *minor* and var. *heucherae* respectively) were usually separable; but there were a few misfits. Having a suspicious

nature, I checked the foliage of all material in DAO, and found that the petiole hairs were reliably distinct, although a few non-fruiting specimens had been misnamed (*Canadian Field-Naturalist* 87: 460–462, 1973). Returning to the mycological specimens all the misfits vanished. These two plants often grow together in the eastern hardwoods, and occasionally the helpful collector had included an inflorescence — but of the wrong plant. Thus recognition of the small but reliable differences between these two plants led to a reliable way to distinguish vegetative material of *Mitella* and *Tiarella*.

10. Coevolution

Although the term coevolution apparently did not come into use until 1964 (Ehrlich and Raven, *Evolution* 18: 586–608), the phenomenon had been considered for more than a decade previously. But its early history is obscure, for it is often uncertain whether there have been reciprocal genetic changes that are the sign of true coevolution or only a more or less random coexistence. However, when one can trace parallel advancing lineages in both partners I think the occurrence of coevolution must be accepted. (See K. A. Pirozynski and D. L. Hawksworth, Chapter 1 in Pirozynski and Hawksworth, editors, *Coevolution of Fungi with Plants and Animals*. Academic Press, London, 1988). Because I have been cited as a pioneer in coevolutionary studies, I must try to review my role in this field. My early observations were mainly aimed at using rust or smut data pragmatically to improve our understanding of plant relationships. In the first summary of my ideas (*Science* 120: 583–585, 1954), I presented the rather miscellaneous conclusions of a few earlier studies. It was shown that the same rust (not merely a morphologically similar one) attacks *Acorus calamus* and *Sparganium eurycarpum*; and that the two plants, despite superficial distinctions, have several anatomical similarities. Following the mycological conclusions (Parmelee and Savile, *Mycologia* 46: 823–836, 1954) *Acorus* has been variously disposed. According to Cronquist (*Evolution and Classification of Flowering Plants*, 2nd Edition, New York Botanical Garden, Bronx, New York, 1988) it differs from Araceae in so many ways that it has been put into a separate family Acoraceae. However, it will probably prove to be very close to *Sparganium eurycarpum*. In this example the rust is useful to the systematist, but there is no very clear sign of coevolution. On the other hand, it was shown that the rusts of Poaceae, Cyperaceae and Juncaceae are, on average, much more primitive than the rusts of Liliales. Some rust clans can be traced through a group of grass or sedge rusts into greatly advanced autoecious liliicolous species. Here there is evidence of abundant coevolution, not all evident in 1954 but increasingly so as time went by.

By about 1960, although most of my papers dealt with detailed taxonomy of various groups of fungi, I was increasingly concerned with that of the host plants; and minor emendations of the latter were occasionally indicated, including: disposition of *Allium* (Mycologia 53: 31–52, 1961; Nature 196: 792, 1962); *Eriogonium* (*Canadian Journal of Botany* 44: 1151–1170, 1966); *Filipendula* (*Brittonia* 20: 230–231); Veroniceae (*Canadian Journal of Botany* 47: 1085–1100, 1969); *Ledum* (*Canadian Journal of Botany* 47: 1085–1100, 1969); *Scirpus* etc. (*Canadian Journal of Botany* 50: 2579–2596, 1972); Saxifragaceae (*Canadian Journal of Botany* 51: 2347–2370, 1973; *Annals of the Missouri Botanical Garden*. 62: 354–361, 1975); Brassicaceae (*Canadian Journal of Botany* 52: 1501–1507, 1974); *Pedicularis* (*Proceedings of the Indian Natural Sciences Academy* 438(6): 223–227, 1977). Several families, including Poaceae and Cyperaceae-Juncaceae, were discussed in *Botanical Review* 45(4): 377–503, 1979. Poaceae was further discussed in Chapter 16 of *Grass Systematics and Evolution*, edited by T. R. Soderstrom et al., Smithsonian Inst. Press, Washington, 1987. Interrelationships of Poaceae, Cyperaceae and Juncaceae, with confirmatory evidence of Juncaceae evolving from Cyperaceae, are discussed in *Canadian Journal of Botany* (68: 731–734).

11. Why are Scientific Advances so Slow?

Fully professional biologists seem to have appeared ca. 1870 in Germany, where the universities were supported by local princes and not controlled by religious sects; and science consequently flourished. In England, on the contrary, Oxford and Cambridge were rigidly controlled by the anglican church until 1871; until then admission was only to anglicans, and all senior staff positions were held by anglican divines. A vow of celibacy for students and teachers was abandoned only in 1878. Even after 1871 individual colleges could, and most did, refuse admission to jews, catholics and protestant dissenters. Thus presbyterians stayed in Scotland where science and engineering flourished; but science stagnated in England, where only brilliant individuals such as Darwin could advance without aid from the universities. According to C. D. Darlington (*The Evolution of Man and Society*, London, George Allen and Unwin, 1969) the same attitude was still common well into the twentieth century; but new universities, and new colleges, free from the religious system, finally allowed great advances.

Independent achievements were ill-received by self-satisfied members of the establishment. When Beatrix Potter, a remarkable self-trained naturalist, discovered the lichen symbiosis she was ridiculed by the learned men of Kew: Not only was she a woman but she was not a university graduate; ergo she could not discover anything. Luckily for generations of

children, she went on to fame and fortune with her animal stories; and the lichen symbiosis was soon rediscovered in Germany.

Professional biology in the United States seems to have developed gradually, perhaps from 1870 to 1890. In Canada, with its small and scattered population, professional training seems to have developed mainly between 1900 and 1910, with delays certainly due in large part to the stagnation of science in England. But in most countries the numbers of professional biologists seem to have been few until about 1920; and progress was understandably slow.

However, even in recent years we do not see one breakthrough leading directly to the next. Why is this so? Are biologists as a whole too slow in their thinking to take faster steps? I do not think so. Consider Stephen Hawking, the theoretical physicist believed by many of his colleagues to have perhaps the finest intellect of the twentieth century. In discussing Hawking's work, John Boslough (1985. *Stephen Hawking's Universe*. Win. Morris, New York) shows that, despite his many contributions, his ideas do not come in a steady stream. After a long period a new idea is born (it may be in the middle of the night) for no obvious reason; then he and his colleagues again pursue the origin of the universe a stage further. Boslough quotes Hawking as saying: "I think we'll come to the unifying theory within the next two decades, probably in a series of small steps. But you know, once we find it, it will rather taken the fun out of theoretical physics." Fortunately biology is so much more complex that we shall surely not lose the fun of it for a long time; but still work hopefully toward that end.

Perhaps we lesser mortals, such as botanists and mycologists, need not be too ashamed of our halting progress; but surely we should try to understand its causes, and then perhaps we may find some remedies. When a theoretical physicist gets a new idea it presumably is born from a particular association of prior ideas. It is like rotating a kaleidoscope to get a new pattern. When a field biologist (i.e. a true naturalist) gets a new idea, or a new understanding, it is often derived from a newly observed structure or mechanism associated with an old idea, or a familiar structure associated with a new idea. When I saw *Tiarella* capsules hit by drops from the canopy I knew at once what was happening because the action of falling drops on splash cups was already in my mind. Would I have understood what was happening if I had seen the plants without having been involved with splash-cups? Well, certainly not immediately; but obviously the mechanism had to be seen in the field to be understood. No one, including myself, who had studied herbarium specimens of *Tiarella* seems to have suspected a function for those "ridiculous" capsules. A character can be "ridiculous" only when we do not understand it. The poet disparages the ragged fingers of a crow; but the crow is large enough to need the extra lift from its wing-tip slots for economical travel even in level flight.

Recognizing the value of field study to clarify a function, let us look at the lamentably slow growth in our understanding of the rust fungi, which was certainly not entirely due to a paucity of students. The history, up to 1928, is told in some detail by J. C. Arthur et al. (*The Plant Rusts*, Uredinales, John Wiley, New York, 1929), with pertinent references. Anton de Bary, an intellectual giant, understood the morphology and parasitism of the rusts as early as 1853; but, despite insistence by farmers of the abundance of wheat stem rust near barberries, he did not countenance the identity of the aecia on barberry with the uredinia and telia on wheat for ten years: The concept of heteroecism was simply too preposterous for an educated man to accept. (Here is a parallel of Beatrix Potter and the lichens: We must have open eyes *and* minds). He finally proved the connection by reciprocal cultures in 1864 and 1865. He then also connected up some other heteroecious species. De Bary's unwillingness to recognize heteroecism in the rusts is curious, for he already knew of the phenomenon in some animal parasites. Although the pycnia were suspected of being spermogonia by Tulasne as early as 1851, there seems to have been little or no progress in understanding them for many years, despite various cytological studies. They are, in fact, a combination of spermogonia, receptive hyphae and a nectary, and are a unique structure whose significance is overlooked by a few workers who call the whole organ a spermogonium. Because the spores did not germinate by germ tube, they were held to be functionless. Surely by 1900 or thereabouts someone should have suspected that a functionless organ would not persist for millions of years in genus after genus. Finally J.H. Craigie (*Nature* 120: 116–117, and 765–767, 1927) demonstrated that insects feeding on the pycnial nectar transferred pycniospores to pycnia of the opposite mating strain, resulting in the formation of dikaryotic aecia. Why did this step have to take three-quarters of a century? Pycnia are prominent in many rusts. I recall in my student days, a few years after Craigie's work, watching assorted insects feeding on the conspicuous pycnia of a *Gymnosporangium* on *Crataegus* leaves. Had no naturalists seen insects feeding on pycnial nectar during all that time?

How was the understanding finally achieved? Craigie's work was done at the then newly founded Rust Research Laboratory at Winnipeg. Craigie must certainly have been influenced by A. H. R. Buller, professor of botany at the University of Manitoba, who, with his intense sense of curiosity, was always interested in the work of other investigators. Staff at the Rust Lab were inclined to give full credit to Craigie, with the inference that Buller was merely in the way. However, Harold Brodie, who was Buller's

student at the time, told me many years later that Buller saw flies visiting the nectar on the inoculated barberry plants in the greenhouse, guessed what was happening, and told Craigie to grow seedlings in insect-proof cages and do controlled nectar transfers. After the successful experiments had been completed he urged Craigie to write it up for *Nature*. According to Brodie, who was working in Buller's office at the moment, the first draft of the note was so unsatisfactory that Buller practically dictated the final version. They have all gone now, Brodie being the last, and we shall never know the truth in every detail. As one who several times saw Buller in action and who later worked under Craigie, I can well believe that in his enthusiasm Buller may have told Craigie what to do (even if Craigie was already doing it). Harold Brodie was meticulous in giving credit, and I therefore believe his interpretation of the scene in Buller's office. However, Craigie was a canny Scot, not to be rushed in any action. He was not a ready writer (or speaker), but would keep polishing a statement and changing adjectives until he was finally satisfied. I recall a memorandum that went between him and me for a week before he released it (little changed from my original, but certainly no worse). Therefore, I would not expect the draft that Buller saw to have been wholly satisfactory: It may have been only a first draft, which Craigie would have polished without help (eventually). Buller, in contrast, seems to have been a very ready writer who never had to revise extensively. Buller had tremendous enthusiasm and considerable imagination; but he seems to have been inclined to dictate experiments to others in preference to doing them himself. (Years later he visualized the splash dispersal in *Cyathus* and conned Brodie into finding specimens and running the tests that provided the splash-cup mechanism).

Next A. M. Brown (*Nature* 130: 177, 1932) demonstrated that uredinial cultures of the autoecious *Puccinia helianthi* could dikaryotize isolated pycnial infections by nuclear transfer following hyphal fusion. In 1939 (*American Journal of Botany*. 26: 585–609). I demonstrated cytologically the fusion of pycniospores to receptive hyphae, including a nucleus in transit and the clear circles left on the wall of the receptive hyphae after the pycniospores fell away. Using advanced staining procedures, including the Feulgen method, I was able to interpret realistically some of the improbable figures that had added mystery to rust cytology (see section 6). Incidentally, I showed that the so-called Blackman and Christman fusions in the aecial fundament have no taxonomic distinction; both types and intermediates may occur in a single aecium, and they represent the shortest available route for an introduced nucleus initiating a dikaryon.

In the meantime, it was widely assumed that rusts without pycnia were evolutionary dead ends, incapable of recombination. One of the conspicuous results of our extensive post-war field program, with its good geographic coverage, was the finding that such rusts are usually morphologically uniform over a widely occupied area; but that geographically isolated populations tended to differ from one another although each was homogeneous. It was clear that genetic recombination was operating in such populations: they were not fragmenting like a fully apomictic dandelion. Then I demonstrated a morphological cline between two subspecies of *Puccinia cruciferarum*, and it became clear that any two adjacent dikaryotic hyphae that are genetically distinct must trade nuclei when they meet (*Mycologia* 56: 240–248, 1964). Finally, the high-arctic *Puccinia poae-nemoralis* ssp. *hyparctica*, isolated by the onset of the Wisconsin glaciation, was seen to differ very uniformly from the parental subspecies in the size, pigmentation, wall thickness and sculpturing of its urediniospores and in its host range (*Arctic Adaptations in Plants*. Canada Department of Agriculture Monograph number 6, Ottawa, 1972). Because *P. poae-nemoralis* never produces telia in the arctic, meiosis cannot be involved; and the accumulation of all the mutations adapting ssp. *hyparctica* to an extremely arid climate can only be accounted for by parasexual recombination, following nuclear transfer.

The jumping of rusts to new hosts also involves their genetic make-up. In 1954, collecting in the mossy coastal forest of southwestern British Columbia, Calder and I repeatedly found *Pyrola* spp. and *Goodyera* spp. growing in close association. *Pyrola* often bore uredinia of *Pucciniastrum pyrolae*; and *Goodyera* occasionally bore pustules of *Uredo goodyerae*, which is excluded from *Pucciniastrum* because it lacks telia, but which has urediniospores only slightly distinct from those of *P. pyrolae*. Except for the scarcely separable *U. ishikariensis* in Japan this is the only such rust on a monocotyledon. Clearly it arose by a jump from contiguous *Pucciniastrum pyrolae*. Although I saw, in the humid coast forest, what had happened, I did not see its full significance and thought it a rare freak. Twelve years later, when revising some rusts of Scrophulariaceae, I recognized another unmistakable jump, by *Puccinia palmeri* on *Penstemon* to *Pedicularis*, with the evolution of *Puccinia rufescens*. Both rusts have the relatively uncommon O, I, III life cycle with repeating aecia, and several conspicuous morphological resemblances; but *P. rufescens* has clearly rugose teliospores, in contrast to the smooth or faintly roughened spores of *P. palmeri*, and is certainly the derived species. With field experience in the Cordillera I saw what had happened. *Penstemon* and the cordilleran *Pedicularis* have strong geographic and ecological overlap; and, although *Penstemon* is clearly a modern genus, the cordilleran *Pedicularis* are even more modern, having evidently originated from a late Tertiary asiatic immigrant and radiated mainly in the Pleistocene when cli-

matic fluctuations tended to fragment populations and stimulate speciation. The conditions that promote a successful jump evidently include strong ecogeographic overlap, a young and genetically diverse parental rust (with a large gene pool), and a young and genetically diverse potential host (younger than the parental host). With these conditions the chance of compatible genomes meeting is maximized. I now realize that jumps have occurred abundantly in the evolution of the rusts. At last it was seen why Dietel's early observation that rusts and hosts reflect each other's ages of origin is valid. Why was it not generally understood for 67 years? Well, it should have been understood after a mere 63 years, but ignorance intervened. A fully documented account of the mechanism and supporting taxonomy was submitted in 1966 to *Canadian Journal of Botany*. Both editor and reviewer accepted the taxonomy but insisted that the discussion be purged (editing by axe!). Eventually it was enthusiastically accepted for *Nova Hedwigia* (24: 369–392, 1968 [1969]). This journal deals with all cryptogams but not spermatophytes, so the paper was not seen by many phanerogamists. The jump mechanism was re-explained in a symposium paper in *Quarterly Review of Biology* (46: 211–218, 1971) where everyone saw it. (I stopped counting reprint requests at about 800). When the mechanism was finally explained it was through my field observations combined with detailed microscopic work. This major step in understanding rust evolution was possible because I was an experienced field naturalist, which is surely how most evolutionary advances are achieved.

12. Progress can be speeded

The answers to problems relating to rust biology, and many similar topics, lie in the need for copious field work, but field work with the eyes and mind wide open. Also the collector should either be involved with the laboratory studies or be in close contact with that person. In this way cause and effect are most easily related.

In my nine full seasons of field work between 1949 and 1962, I doubled as botanist and mycologist both by inclination and by necessity; and the value of this broad approach was soon very clear. At three arctic sites where my stay covered the nesting period (Chesterfield, Isachsen and Hazen Camp), I was able to run a breeding bird census, which gives an approximate measure of biomass productivity. A botanist patrolling an area devoid of tall plants can locate nearly all nests; but such counts are impossible in wooded country. If we go into the field with the responsibility to collect and study ecologically all plants and fungi, *and develop an intense interest in them*, we can scarcely avoid discovering new information about many of them. Apart from the personal satisfaction that our observations give us, this maximum yield of information justifies the substantial cost of keeping a party in the field. Once we have fair coverage of an area, specialized collecting, to complete information in a particular field of study, is justified; but to go into an inadequately studied region with the blinkers on, neglecting all but one small group of organisms, may be worse than useless, making it difficult to promote an adequate attack on that region later.

The wealth of new biological information secured in the years 1949 to 1962 (after which funding for biological exploration was drastically reduced) must greatly exceed that of any previous period in Canada.

Personal field and microscopic study explained how a rust jumped from *Penstemon* to *Pedicularis* (see section 11). Because he had described so many rusts J. C. Arthur received many specimens for study from other collectors; and his field observations became increasingly limited to the vicinity of Purdue University. Studies by others at arctic or alpine treeline have shown the limitations of heteroecious rusts. When Holway sent Arthur the type collection of *Puccinia praegracilis* on *Agrostis thurberiana*, collected near treeline, he sent with it a note stating that it "grew adjacent to the *Habenaria* aecidium, and no where else." Arthur named the rust but later buried it in *P. coronata* because he did not appreciate Holway's warning; but Holway was absolutely right, as I have shown repeatedly. Near treeline these exclusive associations are more reliable than artificial rust cultures in which contaminations do occur. If puzzles are to be solved promptly the collector must include full information and the identifier must not ignore it.

Most of my discoveries in various organisms resulted from field observations made with an open mind conditioned by previous experiences. Field work and microscopic study demonstrated gene flow and geographic races in *Puccinia cruciferarum*, which lacks pycnia. I discovered *P. poeae-sudeticae* ssp. *hyparctica* in arid Hazen Valley because, from experience in arid southern British Columbia, I knew enough to look in the axils of the grass leaves where dew lingers; and its distinctness confirmed the occurrence of parasexual recombination in a rust lacking teliospores (see section 9).

Inspired by H. J. Brodie's seminal paper on splash-caps (*Canadian Journal of Botany* 29: 224–234, 1951), I demonstrated splash-cups in *Chrysosplenium* and *Mitella* (*Science* 117: 250–251, 1953), but was puzzled by the strange capsules of *Tiarella*. Soon after my note appeared, as I stood in the coast forest of southwest British Columbia in a drizzle, I saw capsules of *Tiarella trifoliata* flicker as drops from the canopy hit them, and the operation of this elegant springboard was revealed (see section 9: Fruits of Field Work). Five years later, seeing *Chrysosplenium rosendahlii* spreading freely in marshes on Somerset Island, with only nodding grasses and sedges as a

canopy, I was puzzled at the thought of drops falling only half a meter being effective dispersal agents. Many years later H. N. Hayhoe derived an equation demonstrating the effectiveness of large drops falling very short distances (information important to plant pathologists) and our understanding of splash-cups and springboards was finally nearly complete (section 9).

Among observations on plants apparently originating with me: *Alopecurus alpinus* and *Papaver radicatum* (s. lat.) have such low temperature tolerances that even in the high arctic their growth is limited mainly by aridity. Field observations disproved claims that *Poa glauca* is fully apomictic, when it was found freely crossing and backcrossing with *Poa hartzii* at Hazen Camp, and also hybridizing elsewhere with a member of the *Poa arctica* complex. Other strongly self-fertile plants were shown to outcross on occasion; e.g. hybrids between *Stellaria edwardsii* and *S. laeta* were found at Hazen Camp. I showed that *Saxifraga oppositifolia* was fully self-fertile at Isachsen, two distinct biotypes being present but no intermediates; sustained observations showed that, about two days after the stigmas became receptive, elongation and curvature of the filaments brought the anthers approximately into contact with the stigmas. (The only abundant potential pollinators were chironomid midges, which prefer white flowers and seemed to feed mostly at *Stellaria* and *Cerastium*.) In contrast, at Hazen Camp, which is much warmer in summer than Isachsen, two bumble-bees (*Bombus polaris* and *B. hyperboreus*) were present, and it was difficult to find any two plants of *Saxifraga oppositifolia* that were convincingly identical. At least three biotypes seem to have been present originally and the bees had mixed them freely. Later P. G. Kevan (Insect pollination of high-arctic flowers. *Journal of Ecology* 60: 831–847, 1972) showed that *S. oppositifolia* at Hazen Camp is about 90% self-sterile.

Detailed observations of plant growth at Isachsen, physical conditions, and the total ranges of plants allowed me to interpret the late glacial and postglacial history of the northwestern Queen Elizabeth Islands. The Islands were lightly snow- and ice-covered; in the postglacial hypsithermal interval they were well vegetated; but with increasing cold many plants were eliminated, leaving broken distribution patterns. The islands were not, as once suggested, a glacial refugium (see section 8). Thus the glacial history of the region was completely reinterpreted.

My observations of the Peary Caribou (*Rangifer tarandus pearyi* on Ellef Ringnes Island explained why, in defiance of Bergmann's rule, this is the smallest, rather than the largest, race. Two distantly separated family groups (buck, doe and one fawn) each seemed, from their tracks, to patrol some 700–800 km^2, clipping off plant tops as they moved. As these regions usually have less than 1% of the ground covered by very small plants, continuous movement of the animals is necessary for their survival; and survival is best assured by small body size, which allows reproduction with minimal food intake. The Red-throated Loon (*Gavia stellata*) is the smallest member of its genus and also has the most northerly limits. Here small body size functions by allowing take-off and landing in relatively small ponds that become ice-free promptly. Large lakes, such as Lake Hazen, are used for fishing, but ice-shove keeps the shores bare of vegetation and impossible for nesting (Savile. A naturalist looks at arctic adaptations. *In* Evolution Today, pages 47–53, G. G. E. Scudder and J. L. Reveal *Editors. Procedings of the 2nd International Congress of Systematic and Evolutionary Biology*, Hunt Institute, Pittsburgh).

I spent nine more or less full seasons ($1^1/_2$-4 months) in the field between 1949 and 1962, with shorter periods in two other years. This abundant exposure to the living world obviously contributed substantially to most of my success in interpreting biological (and occasionally physical) phenomena. It should be equally obvious that exposure to the biota cannot guarantee success. One must keep the eyes and the mind wide open. The unperceptive collector can bale botanical year after year and discover nothing — in fact not even see that unsolved problems exist. To break new ground the field biologist must either have an innate sense of curiosity or have been stimulated by associates (I was twice blest), preferably both, for it generally pays to look at several aspects of a problem. The six blind men could not adequately describe the elephant because none would walk round it.

Unusual characters do not evolve randomly; nor do they exist simply to aid taxonomists. If we can recognize their functions we may get clues to the evolution and paleoecology of the organisms. Sometimes the function is obscure except under particular conditions. The team approach may then speed up recognition; but all team members must obviously be alert to the problem. Seed dispersal is a critical problem in most flowering plants. Years of observation in Saxifragaceae (*senso stricto*), a clearly natural group, revealed a surprising variety of dispersal methods, both local and long-range (D. B. O. Savile. Evolution and biogeography of Saxifragaceae with guidance from their rust parasites. *Annals of the Missouri Botanical Garden* 62: 354–361, 1975). It is worth noting that all these mechanisms have also evolved in other plant groups, reminding us that in important problems there may be repetition of one solution as well as multiple solutions. In the large and ecologically diverse genus *Carex* the fruits may be scattered by wind, lodge in the fur or feathers of passing animals, float across water by virtue of bladdery perigynia, or even be ingested by birds as in *C. aurea* with fleshy, sweet and bright yellow perigynia (Savile, *Botanical Review* 45: 488, 1979). The Asi-

atic *C. baccans* Hara similarly has fleshy but red-purple perigynia.

As in flowering plants, dispersal in fungi is critically important, involving many modifications. A long-cycled rust initially has two dispersing spore states, aeciospores and urediniospores, which might seem ample; yet in the three advanced rust families, with pedicellate teliospores, diasporic teliospores have evolved in at least 17 genera by at least 9 methods. Spore release is usually accompanied by newly adaptive changes: nearly uniform rather than apical wall thickening, broadened and shortened spores, sculpturing of spore walls, and a tendency for germ pores to drift from the apical or septal position. In the big genus *Puccinia* (and the related *Uromyces*) I was able to recognize the attainment of deciduous teliospores in more than 30 lineages by six methods of release (Savile. Evolution of the rust fungi (Uredinales) as reflected by their ecological problems. *Evolutionary Biology* 9: 137–207, 1976). Diasporic teliospores must be particularly important in short-cycled rusts; but they have also evolved in 47 long-cycled *Puccinia* or *Uromyces* in North America, and they must therefore be strongly adaptive even when aecia and uredinia are present. J. C. Arthur (*Manual of the Rusts in United States and Canada*. Purdue Research Foundation, Lafayette, Indiana, 1934) divided *Puccinia* into two sections: *Eupuccinia* with firm and *Bullaria* with fragile pedicels. Even in 1954 (D. B. O. Savile. Cellular mechanics, taxonomy and evolution in the Uredinales and Ustilaginales. *Mycologia* 46: 736–761) the functions of the correlated changes in diasporic teliospores were clear and I identified several lineages of *Puccinia* and *Uromyces* that occur in both of Arthur's sections. His sections are thus completely unnatural and taxonomically misleading. Indeed some species have incipiently diasporic teliospores and defy disposition to section. Arthur apparently thought more in terms of a convenient pigeon-holing system, comparable to that of Engler and Prantl for the flowering plants, than of a classification reflecting active evolution in the rusts.

13. Truth and Beauty in Biological Research

What drives the research biologist? Scientists expect to make an adequate living from their work; but if money were their main objective they would be in other professions. Recognition by one's peers, or rarely by the general public, may be satisfactory, but is a result of rather than an impulse to research. Surely we are driven largely by the excitement of discovery and the ultimate delight of establishing a truth built up from a series of observations. Basically we seek to establish facts and, from them, to establish the truth of a system. But truth, for a scientist, goes beyond the bald statement of truth vs. falsity sought in a court of law. Establishing a scientific truth is a matter of great satisfaction, the true picture becoming a thing of beauty. The search for, and demonstration of, truth must surely be the driving force behind all dedicated scientists, whether or not they equate truth with beauty; but the imaginative worker must generally recognize beauty.

Although Keats' statement — "Beauty is truth, truth beauty" — is surely the most famous equation of truth and beauty in English, Chandresekar's essay (S. Chandresekhar. Ph. 4, Beauty and the quest for beauty in science, in *Truth and Beauty: Aesthetics and Motivations in Science*. University of Chicago Press, Chicago and London, 1987) shows us that many people down the centuries have discussed the same theme.

The concept of beauty in truth is surely an important stimulus to the research biologist. Much of his time in the field or back in the lab is taken up by routine collecting, processing or identification of specimens, leavened by unexpected observations or the finding of unexpected species. But once in a while he discovers the function of a character or finds the specimen that explains earlier observations. How wonderful life suddenly is! Such revelations of beauty do not occur very often (just as well, for they can be pretty intoxicating), but they break the routine. The discoveries need not be major, but they clarify a problem, as two examples show. (1) On a drizzly day in southwestern British Columbia. I saw a *Tiarella* capsule flicker under a falling drop; and suddenly its strange form was revealed as a functional and beautifully engineered springboard (Section 9); and it was clear that *Mitella* and *Tiarella* diverged in humid forests from a heucheroid ancestor, each evolving an effective but separate splash dispersal mechanism. (2) When Calder and I were revising the subspecies of *Saxifraga punctata*, we found plants near Prince Rupert that possessed characters of two mainland subspecies but also some of an unknown plant. Suspecting these characters to be from a Queen Charlotte Islands race, we advanced our visit to these Islands. I can think of few more rewarding moments than when, after struggling up Tan Mountain, we first saw *S. punctata* ssp. *carlottae* looking exactly as we anticipated.

It has been suggested that its aesthetic value may justify a theory that is shown to disregard facts; but surely an honest scientist cannot support such an idea. If a theory is false it is so defaced that, to me, it immediately loses any beauty. However, it is sadly true that some workers find it difficult or impossible to discard an old belief despite accumulating evidence against it. Although it was plain even in 1954, partly from parasite data, that Liliales are younger than Poaceae and Cyperaceae, a few authors have even recently indicated them to be older (e.g. A. L. Takhtajan. Outline of the classification of flowering plants, oragnoliophyta. *Botanical Review* 46: 225–359, 1980; R. M. T. Dahlgren and H. T. Clifford. *The Monocotyledons: A Comparative Study*. Academic Press, London, 1982).

Biology differs from the physical sciences in several respects. In physical sciences simple laws are applicable because the systems are simple. In biology, as Ernst Mayr has shown more than once, the systems are infinitely complex: All the molecules of a chemical compound in the universe are identical; but in sexually reproducing organisms no two individuals, except identical twins, are ever the same.

The physical scientist, often after years of labour, produces laws or principles that are applicable because the systems are simple. Chandresekhar indicates that most physical scientists make their major contributions early in life; and he contrasts them with great poets, writers and musicians, who often produce very fine works late in life. It is notable that many biologists show a pattern similar to that of workers in the arts. Charles Darwin published *The Origin of Species* (his first major work) at age 50; and his other volumes appeared during the next 24 years. Ernst Mayr, born in 1904 and arguably the greatest evolutionary biologist of this century, has been publishing on evolutionary topics continuously since 1940, with important books appearing in 1942, 1963, 1970, 1976, 1982 and 1988. Many other biologists of my acquaintance have continued in productive research to formal retirement and beyond, as long as their health permitted.

A biologist's main contributions may all be made relatively late in life, as was true of Darwin, simply because accumulating countless small observations and fitting them into a useful and informative structure inevitably takes a long time. This tendency reflects the complexity of biological systems. The young field biologist collects specimens for taxonomic study, and records their geographic range, general ecology, habitat (with orientation and altitude where pertinent), and associations. Eventually all these bits of information will lead to a broader understanding of the biology of the organisms. Thus we may often pass most of our careers before we are prepared to present a complete picture of a topic. But, because we are dealing with living and genetically variable organisms, the picture is seldom really complete, and in later years we, or others, will add to and modify it. There can be no mathematical proof that the picture is correct, for the pieces of the puzzle may change in shape and numbers at any time. What we aim at is the simplest explanation that conforms with all the data. If the data are abundant the most parsimonious solution is nearly always correct; but we are dealing with probability rather than mathematical proof. As time passes we generally discover additional pieces to fit into the puzzle; and the probability of a correct solution finally becomes enormous and can be accepted.

About 1973 I started to assemble observations, which I had been accumulating for about 30 years, into a paper on evolution and ecology of the rusts (D. B.O. Savile. Evolution of the rust fungi, Uredinales, as reflected by their ecological problems. *Evolutionary Biology* 9: 137–207, 1976). When I finished it late in 1975, I hoped that the story was reasonably complete. Scanning my annotated copy I see considerable additional information from more recent publications, but nothing to change the main conclusions. Thus the timing was evidently appropriate. If I had attempted it many years earlier it would have been very inadequate; and if I had delayed it for more than 10 years I probably could not have achieved it, because of other involvements.

When Arthur Cronquist suggested, in 1977, that I write an article for the *Botanical Review* on fungi as aids in plant classification, I had no illusions about a complete treatment, for much information is buried in papers whose titles and abstracts contain no appropriate key words. However, by postponing the attempt until after a related symposium at Uppsala in 1978, I was able to present considerable information in this field. I also made a few discoveries; one that surprised and excited me was that three rust lineages that arose in lower Cyperaceae reached their greatest morphological advancement not only in *Carex* (as expected) but also in *Juncus* or *Luzula*. As the lineages are based on several correlated characters, and the trends in morphological advancement are widely recognized in other rusts, the age and relationship of Juncaceae, as an offshoot of Cyperaceae, seemed incontrovertible. As Juncaceae have been classically accepted as ancestral to Cyperaceae, the indication of their advanced position is understandably unpopular, and was disparaged by two recent authors who, however, attempted no other explanation of the data. The multiple morphological characters of each rust lineage make it extremely unlikely that random similarity would occur even once, the probability being surely at least 100:1 against duplication. That it should occur three times is really unthinkable. Elementary probability tells us that in repeated similarities the odds are multiplied. Thus the odds against random duplication in all the lineages are at least 1 000 000:1. However, in a recent restudy of these families (D. B.O. Savile. Relationships of Poaceae, Cyperaceae and Juncaceae reflected by their fungal parasites. *Canadian Journal of Botany* 68: 731–734.) I found that a smut, *Entorrhiza caricicola*, occurs on *Eleocharis gracilis*, *Carex* spp. and *Juncus* spp., further indicating and advanced position for *Juncus* and relationship with *Carex*. The paper dealing with this and related smuts (J. M. Fineran. A taxonomic revision of the genus *Entorrhiza* C. Weber. *Nova Hedwigia* 30: 1–68, 1978, received in Ottawa 9 April 1979) appeared too late to be incorporated in my *Botanical Review* paper. However, the host range of *E. caricicola* causes the odds against random similarity in the parasites Juncaceae and *Carex* to be perhaps 100 000 000:1. It would probably be hard to find a biological conclusion closer to mathematical proof than that!

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Book Reviews

ZOOLOGY

A Field Guide to the Birds of China

By John MacKinnon and Karen Phillipps. 2000. Oxford University Press, New York, Don Mills, Ontario 586 pp., illus.

Ornithologically isolated for decades, China now welcomes a growing trickle of birdwatchers. With a species list of over 1300, 100 plus endemics and some of the worlds' most impressive birds, including 62 species of pheasant and nine cranes, it's not hard to see why birders flock to China. But China has long suffered from the lack of a good field guide. This situation has now been rectified by the publication of this niche-filling book.

The Birds of China follows a standard format, with a short introductory section to familiarize the reader with the area covered (which includes Taiwan and Hong Kong), the history of ornithology in China, and key conservation challenges, including a depressingly long list of endangered species. For the non-sinologists, the political map inside the back-cover is critical to understanding species distributions. A particularly useful feature is a listing of birdwatching and conservation organizations. The 128 colour plates are grouped together at the front of the book, followed by the species accounts. Each species account includes a brief description, and notes on voice, range, distribution and status, and habits. A Chinese version is planned and the current edition features Chinese names.

The text is terse and to the point. The species accounts will generally be sufficient to identify most birds seen, including difficult groups such as snipe, but suffer from an inconsistent use of vague terms such as the "smallish" Common Tern at 35 cm and the "medium-sized" Black-napped Tern at 33 cm. Some of the more complex species will remain a mystery if this book is your only reference, for example, immature *argentatus*-type gulls are declared unidentifiable. Some of the descriptions are overly simplistic; one would be foolhardy to identify a female rufous-tailed Robin on the basis of its rufous tail alone as several similar species share this feature. That said, there is plenty of great information in this book that is bound to come in handy some day: how many people know that Asiatic House Martin has black wing linings that differentiate it from its European counterpart?

What about the plates? As is often the case in guides covering mega-diversity regions, the quality is variable. Some of the passerine plates are very good; the robins, buntings, pipits, and larks are excellent, a fact which should make sorting out the little brown jobs that much easier. The quality of the non-passerines plates is generally not as good; the gulls are remarkably poor. Nonetheless, many of the paintings show important fine details such as the difference in primary projection between Pacific and American Golden Plover. While a great attempt has been made to illustrate major forms and plumages there are omissions, for example, basic and alternate Teminck's Stints are illustrated but not the immature plumage.

Some paintings, and in particular the large waterfowl, have suffered through excessive shrinking caused in scaling them down to fit the book's format. Generally the colour separation is good, although in the review copy the green tones on one of the leaf warbler plates (plate 99) is much too strong. The arrangement of species on the plates is sensible and the paintings are numbered, making it easy to figure out which species is which. The facing page to the plates feature useful and easy to read colour range maps, however, this arrangement comes at the expense of the helpful identification pointers that are a feature of other major field guides. Some odd birds are left out the plates, including Ibisbill which receives only a line drawing, surely one of the country's most sought-after birds.

One of the strongest features of the book is the fact that it actually is a field guide. While too hefty to fit in most people's pockets, at 20×14cm, and 4cm deep it can easily be tossed into a backback, and it benefits from easy to read type and a generally reader friendly format. The binding and covers are rugged and will probably stand up to usual field use. Some of the printing was blurred in my review copy.

Unfortunately, this book suffers from serious proof-reading problems; it is littered with typographical errors, some of which will cause confusion. For example, the phalarope range maps are mislabelled, the Pied and Collared falconet are reversed, and the text incorrectly indicates that there is a painting of Southern Grey Shrike. Additionally, some of the range maps are suspect, for example, Crested Shelduck is shown with a far more extensive range in northeasern China than the handful of records and questions over its continued survival would warrant: a question mark in the general area of the historical sightings would have been preferable. These mis-

takes are frequent enough that some second guessing is required; hopefully they will be addressed in a future addition.

The taxonomy follows Sibley and Munroe's 1990 *Distribution and Taxonomy of Birds of the World.* While it is a safe bet that the taxonomy of the relatively poorly known Chinese avifauna will be in a state of flux for generations to come, the insertion into this guide of a polemic on the merits of the phylogenic versus the biological species concept is a bit misplaced; perhaps better left for the more arcane journals.

This book will inevitably be compared with recently released volumes covering other megadiversity regions such as India and Kenya, and will suffer in the comparison. Part of this is due to the authors' commitment to producing a book that is truely a field guide: in scaling back the text the authors have lost the sort of detail that some readers will be looking for. Nonethless, the bottom line is that the authors have produced an invaluable book that fills a major gap. This is not a state-of-the-art book, but it is an important birding and conservation tool; this is the first time some species are illustrated in a popular field guide. Indeed, here for the first time I have seen an illustration of one species on my life list, Chestnut Bulbul.

If you are planning to birdwatch in China, this book is a must. If you dream of finding asiatic vagrants on your next trip to Alaska, bring this book along. If you are a avid birding book collecter who hasn't been able to sleep nights worrying about the lack of guides for the oriental region, you should buy this book.

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MARK GAWN

1354 Viking Drive, Ottawa, Ontario K1V 7J6 Canada

The California Condor: A Saga of Natural History and Conservation

By Noel Snyder and Helen Snyder. 2000. Academic Press, San Diego. 410 pp., 124 colour plates, 4 maps, 8 graphs, 23 tables. U.S. $29.95

This large, beautifully-illustrated, fact-filled book introduces us to heroic people and intersperses triumph with tragedy. It is the well-researched history of a remarkable bird and a superb conservation story — of a large bird and all the people who studied it.

Only when a material object like a British Guiana penny black postage stamp, or a bird such as the California Condor, becomes extremely rare, are we willing to spend large sums of money. In the case of the California Condor, the efforts were perilously close to being, at first, too little. More recently, the expenditure of more than a million dollars a year has been almost too late.

The California Condor's wingspan of nearly 3 m is the largest of any North American bird species, and allows it to soar almost continuously. Archaeological evidence includes bones of 63 condors at one human site in Oregon, well north of its 20th-century range. Numerous aboriginal tribes employed condors in ritual sacrifice, perhaps one per village per year in the San Diego region. Others were shot for their quills.

The condor declined further, beginning in the 1870s, when the use of strychnine and later cyanide of potassium were used to kill mammalian predators. Collectors also took a heavy toll, including at least 20 birds and 7 eggs taken in 1897-98 alone. Killing or collecting condors or their eggs was made illegal in California in 1905.

William L. Finley made the first serious study of condors, found his first nest in 1906, and took 250 photographs. Finley considered that condors were extremely tolerant of humans. Carl Koford began his condor studies in 1939, identified their main nesting and roosting areas and estimated that by 1950 only 60 condors remained; in retrospect, the Snyders estimate that there were then about 150. Koford showed that young fledged at about 145 days of age, and then were dependent on parent feeding for another 6 months. He claimed that condors were incredibly shy and sensitive, completely intolerant of the presence of humans, and recommended that a large sanctuary be established to protect them.

A full-time condor warden, John Borneman, was hired by the National Audubon Society (NAS) in 1965. The condor received protection under the Endangered Species Acts in 1966 and 1973. Fred Sibley began four years of condor studies for the U.S. Fish and Wildlife Service (USF&WS) in 1966; with his "superhuman" endurance, Sibley roped down every likely-looking cliff to find both active and many former nest sites. The 1966 condor count showed at least 51 still alive, but detractors claimed, without foundation, that Sibley's close approaches to nests had caused the species to cease reproduction.

In 1968, Sanford Wilbur replaced Sibley and began putting out carcasses as supplementary food for condors. Wilbur led a Recovery Team which pro-

duced a Recovery Plan in 1974 and a Contingency Plan in 1976. Wilbur also supported the appointment of a joint panel of the American Ornithologists' Union and the NAS, which reported in 1978, and was endorsed by the Fish and Wildlife Service. The NAS successfully lobbied Congress to expand the condor conservation effort in 1979. Noel Snyder of USF&WS and John Ogden of NAS developed a new intensive field effort in 1980.

Meanwhile, Friends of the Earth opposed any "hands-on" activities and branded radiotelemetry as "mutilative biology." The unfortunate death of a struggling condor chick strengthened their argument.

In 1981 an ingenious flight photograph file was developed for each condor, using missing feathers to identify each individual. The wild condor population numbered 21 in 1982, 14 adults and 7 immatures. It then dropped precipitously to 19 in 1983, 15 in 1984, and only 9 in 1985. In October 1982 the first free-flying condor was caught safely in a cannon net, blood samples taken and a radio-transmitter applied; eight other wild condors received radios, seven of them in 1984.

Snyder found surprises. Older condor nestlings were fed every 10 hours on average, though 13 times in 605 days of observations the chick went two days without being fed. An individual adult might incubate the single egg for up to 10 days before accepting relief from the mate. Pairs changed nest sites each year, moving an average of 3.8 km to the new nest. Individual condors ranged so widely that they were familiar with the entire range of the population; an individual might fly up to 225 km in one day. Snyder quickly realized that the great wariness of the species is a myth, perpetuated in part to support the sanctuary ideal.

In spite of occasional predation of the single condor egg by Common Ravens, and one egg that rolled out of the nest because of its sloping floor, productivity during the 1980s study (7 or 8 nests successful in 17 analyzable nesting attempts) was satisfactory. Snyder found the decline in numbers, contrary to general belief, was fuelled by excessive mortality, about 25% per year for adults and immatures alike, mainly from lead poisoning. The radios did not contribute to mortality; indeed, only 3 of 9 radioed birds died whereas 12 of 15 non-radioed birds disappeared. Genetic studies of blood samples indicated low genetic diversity in the small remnant population.

An observation in 1982 that, after loss of an initial egg, a condor laid a second after 40 days, allowed a bold experiment of replacement clutching. Beginning in 1983, each wild pair had their first egg taken from the nest and incubated artificially, thus developing a captive population in two zoos, for eventual breeding purposes. The condor was then allowed to raise its second young in the wild. Between 1983 and 1986, 13 of 16 eggs taken in this way produced surviving chicks. Counting those eggs hatched in incubators and those in the wild, six young were raised in 1983 and seven in 1984.

Controversy about taking adults into captivity swirled between the Recovery team and the USF&WS; the latter organization "vacillated between moments of true wisdom and courage and unfortunate lapses in resolve and insight." However, with the catastrophic mortality of six condors during the winter of 1984-85, and lead poisoning of another in December 1985, the official Recovery Plan suddenly became irrelevant. All wild birds were trapped and taken into captivity. By then, the stress of seven years of political duels had taken its toll and Noel Snyder had left the Service, for a "much less confrontational existence."

By 1987, in the Los Angeles Zoo and the San Diego Wild Animal Park, there were 14 females and 13 males in captivity, most fortunately an even sex ratio. In captivity, the level of productivity "far exceeded even the most optimistic projections." The population grew rapidly to reach 150 by 1998. Fertility improved with each bird's experience. By 1999, all 27 birds had been involved in production of at least one fertile egg!

The release of condors back into the wild, based on success with Andean Condors, has not yet been an unqualified success. The release territory still contains carcasses of animals killed with lead ammunition. Puppet-reared nestlings cannot perfectly mimic adult condors in behaviour. When released into the wild, these birds approach humans without fear, enter towns, perch on buildings and poles, and trash property ranging from satellite dishes and roof shingles to screen doors, a habit unknown to former wild condors.

Clearly the parent-reared birds have done best after release: 16 of 21 are still alive in the wild, while only 33 of 67 puppet-reared birds are still alive. Hunting with lead bullets is still allowed in condor release areas, and three released condors have developed lead poisoning, one requiring recapture and chelation therapy to clear its body of much of the lead.

Snyder presents a forceful case that only the new TTB (TinTungstenBismuth) ammunition should be allowed in condor territory and that the maladapted condors in the wild should be recaptured and used again as breeding stock. Sadly, only 7 of 18 young condors raised in captivity in 1999 were parent-reared. Snyder recommends that only nestlings reared by live adults should be released in the years to come.

The situation deteriorated further after the book went to press. At the AOU meeting in St. John's, Newfoundland, in August 2000, Noel Snyder told me that the mortality rate of released birds is excessive, with 20 birds lost in the past year, almost equal to the number (22) produced in captivity in the same period. To date, five released condors are known to have died of lead poisoning while another 16 acutely poisoned with lead have only survived because of

emergency chelation therapy. The cause of death for more than half the birds lost is unknown, since many were never recovered.

Noel and Helen Snyder call a spade a spade, providing one perspective on a complex situation. They recount the deep rift between two camps, the traditional "hands-off" conservation philosophy adopted by the followers of Carl Koford, and the activists who favoured captive breeding. I have one complaint; the heavy paper that allows near-perfect photographic reproduction makes this book too heavy for comfortable handling while reading in bed!

At this incredibly low price, you can buy one copy for yourself and another for a friend concerned about endangered species. This book is a landmark study that must be consulted by those involved in any recovery program for any endangered bird species, in the hope that mistakes made with the condor need not be repeated.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8 Canada

Mammals of North America: Temperate and Arctic Regions

By Adrian Forsyth. 1999. Firefly Books, Willowdale, Ontario. 352 pp., illus. $40.

This is a book any naturalist would be proud to have on his or her bookshelf. Highly readable, visually stimulating with outstanding photographs gracing nearly every page, and filled with fascinating information, it's a resource I know I'll consult again and again.

The author, Adrian Forsyth, an Ottawa native, well-known natural science writer, and Senior Biodiversity Scientist based at the Smithsonian's Museum of Natural History in Washington, has created a unique North American mammal resource. It's partly a field guide offering the following information on each mammal species: names, meaning of the scientific name, general physical description, colour, total length, weight, gestation period, total number of offspring, age of maturity, longevity, diet, habitat, and even dental formula. Unlike field guides, this book does not provide a visual representation for each species.

Yet a number of mammals — the more widespread and/or often better-known species such as the masked shrew, little brown bat, snowshoe hare, groundhog, deer mouse, red fox, black bear, harbour seal, mink, bobcat, beluga whale, elk, and many more — are given a more in-depth profile. These profiles offer deeper insight into the animal, from distinctive features and behaviour, to its ecological role and threats to its survival.

Readers will meet a social shrew, a mouse that howls like a wolf, a seal that naps on the ocean floor, a skunk that climbs trees, and a whale that sports the world's largest tooth. Readers will learn how male deer mice go about providing parental care to their offspring, why racoons wet their food, how the Arctic fox keeps its feet from freezing, why white-tailed deer flash the white of their tails, and how the matriarchal structure of the orca whale works.

Scattered among the species descriptions and portraits are other brief essays on topics as diverse as mammal infanticide, migration, rumination, scientific nomenclature, co-operative hunting, mammal milk, learning at play, bioconcentration of pollutants, and the advantages of eating meat. I was surprised at the cost of growing antlers, the success of the bat (*Chiroptera*) family, and the energy requirements of a harem bull elephant seal. I was impressed by the polar bear's hunting strategies, the sperm whale's diving capacity, the sensitivity of the kangaroo rat's hearing. I was distressed by the references to species decline, habitat loss, and the general insensitivity of our own species.

But above all, I was fascinated, from cover to cover.

As Forsyth writes in his introduction: "This book is a small attempt to interest readers in the wild mammals that live around them. It is generally true that the more one knows about something, the more one wants to know. And to conserve another organism, even to want to conserve another organism, knowledge seems necessary. This is my agenda."

The agenda worked with me. I learned a lot from this book — particularly how complex the world of mammals is, and how much I don't know. So I'm intending to find out more. And I learned, I think, that Forsyth is a modest individual, because this book is anything but a "small attempt." It's a big book, an enormous accomplishment, and a significant achievement.

R. SANDER-REGIER

RR5 Shawville, Quebec J0X 2Y0 Canada

Snipes of the Western Palearctic

By Richard Rouxel. 2000. Eveil Nature, Saint Yrieux sur Charente, France. 304 pp., illus. English or French 215FF.

This book is a detailed scientific review of the published information on the Common Snipe *(Gallinago gallinago)*, Jack Snipe *(Lymnocryptes minimus)*, and Great Snipe *(Gallinago media)*. It does not include Pintail Snipe *(Gallinago stenura)*, which live at the western edge of the Western Palearctic, between the Pechora and Chornaya River basins across to the Urals (Russia). Nor does it include a discussion of Common Snipe in North and South America, although many North American texts are cited (particularly Tuck's CWS monograph on snipe). In addition, it does not clarify the status of an African subspecies of Common Snipe mentioned in the EBCC Atlas of European Birds (often considered full specie – *G. nigripennis*).

After an introduction to the taxonomy of Charadriiformes through to the Gallinagininae, the author begins on the species accounts. About half the book is devoted to the Common Snipe and the balance split between the other two species. Each account contains a very detailed description of these birds. This is literally a feather by feather description of the important feather tracts that might help the researcher determine age and sex. These descriptions also include the molt sequences. Other biometrics such as measurements and weight contribute to information that could be used on captured birds. Most of this material would not be useful for field observations. The section on voice, however, is more helpful for field identification.

The section on breeding is heavily weighted on distribution and numbers. For Europe the breeding population is estimated at 800 000 to 1 000 000. Adding in the Russian estimate of 1 to 10 million makes the range of the estimate a little absurd. Nesting, egg-laying and nurturing chicks is also described in detail.

The movement of birds both diurnally and on migration leads to population estimates and a solid discussion on the validity of the data. This is then linked to mortality, particularly hunting. From even a cursory glance it is obvious that northern Europe is the snipe "factory" for hunters located in southern Europe.

This pattern is followed for all three species of snipe. There is less information on Jack Snipe, presumably because of its secretive nature. There is somewhat more on the Great Snipe, which at least can be counted during its lek displays. As the Common Snipe is the most abundant, widespread, and studied, it accounts for the largest portion of the book.

The book is illustrated with coloured photographs of the birds and their habitat. While the quality of the photographs is good the printing is less so. This is surprising as the paper quality and text printing is very good.

This book is most difficult to read. It was originally written in French. The problems originate from several factors arising from the translation. I am well aware of the difficulties of changing languages. I have access to a very skilled group of translators who, not only are bilingual, but also have extensive experience in the technical and idiomatic language of my domain. They make sure the sense of my text means the same in either language. With this book I think the principal problem is the translation is too literal. This made the sentences convoluted and rambling. In some cases I could see the French version behind the English words and I could better comprehend the sense. Often, though, I got lost and had to back track. This was particularly true of passages involving lots of data and multiple theories on interpretation. I have never seen so many colons in English text before. Their use extended the run-on nature of the sentences.

There were a number of misused words. The prime example is the plural of snipe is snipe and not snipes. Another example is changing the French migrateur to migrator (which is not in my Oxford English Dictionary) instead of the correct word, migrant. Snipe do not browse or pasture, but feed. Pointer dogs "point" or indicate the location of birds; they do not block. The translator mixes quills up with feathers. The North American Marsh Hawk (*Circus cyaneus*) is confused with the European Marsh Harrier (*Circus aeruginosus*) when quoting from Tuck. There are errors of sense too. For example, "must be" is used in places where "ought to be" would be more appropriate. The author or translator uses some correct but obscure words like "haulm" (stems and stalks of plants). As a final comment I noted several typographic errors. While none of these items prevent the reader from understanding the text, they do make that task very difficult. So this book is a very detailed compilation of the current knowledge on the three snipe species but ... A mon avis ça serait mieux d'acheter ce livre dans la langue originale.

ROY JOHN

2193 Emard Crescent, Beacon Hill North, Gloucester, Ontario K1J 6K5, Canada

The Nature of Spiders, Consummate Killers

By Adrienne Mason. 1999. Greystone Books, Douglas & McIntyre, Vancouver. 128 pp., illus. $34.95

This book is an excellent introduction to the world of spiders. It offers clearly written information, detailed drawings to support certain material, and lots of superb photos. I would venture to say that nearly half the book consists of photographs.

With so much of the book devoted to photography, it still manages to convey an awful lot of information about spiders, including a summary of the major spider groupings (in the first chapter and in a 4-page appendix), descriptions of spider body parts and functions, a glimpse into various courtship and reproduction rituals, and a look at life after hatching, followed by a profile of different types of spider colonies. The book also provides an overview of diverse hunting techniques — including spitting, fishing, lassoing, stealing, and trapping through a wide range of webs — plus a look at creative strategies for spider self-preservation. It addresses the relationship between humans and spiders, from the spider's role in folklore and mythology, to spider conservation and threats to survival.

The author — trained as a biologist, now working as a freelance writer and naturalist — imparts to her topic a sense of awe that comes through in the first paragraph of the book: "Wherever you are, there is a spider within a meter of you ... We share our planet with close to 38,000 known species of spiders, and their diversity is remarkable. Whereas approximately 4,000 mammals roam the earth, there are close to 4,4000 species of jumping spiders alone."

In the pages of the book, readers meet some fascinating members of that 38,000- strong arachnid clan, including the world's largest spider, the goliath bird-eater (*Theraphosa blondi*) tarantula, whose legs could span a small pizza; the European cob-web weaver (*Theridion sisyphium*), who cares for her young by feeding them regurgitated food; fishing spiders (*Dolomedes*) who appear to use the ends of their legs as lures; jumping spiders (*Salticidae*) who let out silk to act as a bungee cord while they capture insects in flight; and the wheel spider (*Carparachne aureoflava*) who flips sideways and cartwheels down sand dunes to escape predators.

The author's fascination for her subject continues throughout the book, coming out as profound respect in the last paragraph, where she puts the spider's future on this planet into perspective: "Long after we have cut our last tree, drained our last wetland, or perhaps even populated ourselves out of a home, somewhere, I have no doubt, spiders will be spinning. Their diversity, industry, and skill seems without parallel; after 400 million years, they have secured their place as one of nature's most successful terrestrial animals." Comforting thoughts.

This book would make a wonderful addition to any naturalist's library, if only for the photographs. The information covered will satisfy the curiosity of anyone wanting to know more about spiders, and will whet the appetite of budding arachnophiles to know more.

The only thing I don't like about this book is the subtitle, *Consummate Killers*. It sends an unnecessary message of ferocity that will not help the spider overcome its unfortunate reputation.

R. SANDER-REGIER

RR5 Shawville, Quebec, J0X 2Y0, Canada

ENVIRONMENT

Encounters With Nature: Essays by Paul Shepard

Edited by Florence R. Shepard. 1999. Island Press, Washington. 200 pp. $38.50.

Until his death in 1996, Paul Shepard, Professor Emeritus of Human Ecology at Pitzer College and Claremont Graduate School in California, wrote twelve books and many essays for publication. His work spanned five decades and his thoughts on human ecology and the relation of humans to the natural world had global perspective. This book compiled by his wife Florence contains essays and book parts written throughout his career with some previously unpublished notes and parts of manuscripts.

I had never heard of Paul Shepard, but I found the material quite readable, entertaining, and thought provoking. His thoughts are critical of the human condition when referring to the natural world, which we share with animals, critical of human perceptions of animals and the world of nature. We have shaped our world in myth, art, children's stories, and popular culture but have not always represented other values besides our own interests when seeing a beautiful picture, a productive land, or cuddly creatures.

Part one of the book deals with animals, hunting, and human judgements. The section on bears is particularly interesting as it examines current ideas and images, the myths of indigenous peoples, and children's toys. Another chapter examines the writings of Dr. Albert Schweitzer, the physician, theologian and missionary in the jungles of Africa. Schweitzer's *Reverence for Life* is critiqued as a European barnyard ethic, protecting those animals which are to be husbanded for consumption and profit, while

destroying predators and pests. Shepard contrasts the perspective of a naturalist with the attitudes of agriculture and profit-motivated animal husbandry.

The second part of the book is a series of essays on the importance of place. Shepard is outraged at how the modern world has taken industrial values and promoted the place of industry as pleasing and attractive. As the director of Green Oaks, the Knox College (Illinois) biological field station where he spent much time replanting trees, indigenous aquatic flora and fauna, and restoring fields to tallgrass prairie, and as conservation chairman for the National Council of State Garden Clubs he had much opportunity to see the changes which industry made on landscapes. In Shepard's discussion industry includes manufacturing, mineral extraction, agriculture, forestry, and pasturing. His essays contain experience from around the globe and insight into the movement of people, their domesticated animals, extraction industries, and building strategies over the millennia.

We need generalists like Paul Shepard with education in many disciplines to look at the big picture and research the interconnectedness of our world. I find that his research informed me on several different levels and his insight validated my experience. Industrial sites are not pleasing to the eye. Hunters are not always evil. Pastoral landscapes are only pleasing in art when your life experience of agriculture has to do with pasturing grazing animals. Overgrazing by sheep and goats is not a biblical value even though it seems to have been the normal practice (and still is) in the Middle East. Our society has forgotten or lost our reverence of searching and finding game, indigenous plants, nourishment, and shelter given to us by the earth and its Creator. Paul Shepard calls us back to that reverence in his cynicism of the ways we delude ourselves and in his outrage at our wrong directions. I enjoyed the book, was able to identify with human ecology as he presented it and have discussed ideas from it with many friends. I recommend it to you.

JIM O'NEILL

St. Mark's College, 5935 Iona Drive, Vancouver V6T 1J7, Canada

River in a Dry Land: A Prairie Passage

By Trevor Herriot. 2000. Stoddart Publishing, Toronto. 356 pp., 2 maps. Canadian $34.95.

Trevor Herriot, a naturalist, writer, and artist, spent part of his early childhood in and near the eastern end of the Qu'Appelle Valley, Saskatchewan. The valley is deeply rooted in his soul.

This, his first book, is a tribute to the valley, its first peoples, its flora and fauna, and much more. Herriot takes us on an unusually personal journey, an exploratory tour with no holds barred. He mixes with admirable skill his observations on geography, geology, history, archaeology, anthropology, agrology, sociology, philosophy, economics, botany, mammalogy, and, his great love, ornithology. And throughout and above all, he demonstrates superb ecological insight and wisdom remarkable for a man so young.

Herriot sees the world through the eyes of an artist, offering vivid word-pictures, writing with nostalgia but also with sensitivity and integrity. His lyric, sometimes poetic prose ranks him as the successor to Wallace Stegner. His book should place Tantallon and the valley on the map, equivalent to Stegner's success in Wolf Willow that placed the Cypress Hills and Eastend in public view.

The dust-cover blurb is "right on" when it says "Herriot blends personal memoir and natural history and family legend with social commentary. ... generations whisper to generations, in the voices of early explorers and utopian colonists, archaeologists and Cree elders, homesteaders and geologists. Their words arise always at the side of pathways both ancient and modern; the footpaths of buffalo hunters, the cart trails of displaced Métis and land-hungry immigrants, the spoor of coyote and bear, the rail lines abandoned by the very economy that built them, and, of course, the wandering, eloquent lines of the river itself."

Herriot's broad sweep covers the entire Qu'Appelle watershed, from Canada's first wildlife preserve at the north end of Last Mountain Lakesouth to the former brick plant at Claybank, and from the west end adjacent to the South Saskatchewan River elbow, to the east end of the valley where it joins the Assiniboine River near the Saskatchewan - Manitoba boundary.

Because he tells the truth, some of what he says may cause resentment among those who worship the almighty dollar and confuse prosperity with progress. The first peoples of the valley and their relatives the Métis, with an ethic of local subsistence, were seminomadic. In contrast, Caucasian settlers, fixed to a half-section or section of land, were dependent upon distant economies and after a century or less left their farms, as Herriot says, "in the next movement to prosperity, better land, better jobs, a better El Dorado." We are "exporting the life of the soil that fed the buffalo and prairie peoples in a sustainable cycle over thousands of years. ... We have too few farmers using too much machinery to feed too many people too cheaply too far away." He catalogues

much evidence of the white man's short-sightedness and stupidity. He vacillates between extreme pessimism and cautious optimism, and offers only a faint ray of hope for the future.

On the credit side, as Caucasian farmers increase their individual holdings and their numbers become fewer, there has been an increase in elk, bears, ravens, and eagles.

We learn about many people, including: the explorers, David Thompson, John Palliser, Henry Youle Hind; the poet, Pauline Johnson; early naturalists, John Macoun and R.D. Symons; the lifetime chronicler of valley bird life, Manley Callin; and Professor Zenon Pohorecky, who tried to preserve Mistaseni, the giant 400-ton buffalo rock, sacred to the Cree. We are also told about the short-lived Hamona colony, which failed because not everyone contributed equally to the farm labours and because the promised railroad failed to materialize; breadroot, wild onions, wild turnips, seneca root, the sources of natural food and medicine; the two species of towhee and two species of wood pewee, whose ranges meet in the valley; the endangered Burrowing Owls and Piping Plovers, the declining Upland Sandpiper; Swainson's Hawks and Richardson's Ground Squirrels. Recurring themes include the Bank and Barn Swallows and Say's Phoebe.

A review such as this can only hint at the superior quality of writing, especially Herriot's ability to meld and synthesize a wide range of topics. This gifted wordsmith will provide many unexpected pleasures and provoke thought for any reader. A best-seller, appealing to a wide audience, it made the short list for the Governor-General's award for non-fiction. Reprinting was necessary less than three months after its release, in spite of a substantial first printing run. This book is the perfect gift for any naturalist and for anyone who wishes to learn more about Saskatchewan.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8, Canada

MISCELLANEOUS

Yellowstone and the Great West: Journals, Letters, and Images from the 1871 Hayden Expedition

Edited by Marlene Deahl Merrill. 2000. University of Nebraska Press: 315 pp. U.S. $29.95, £19.95.

The US government's surveys of the American West rank among the great scientific endeavours of the nineteenth century. In assessing the American frontier's potential for commercial development, these surveys were a form of applied science with a government subsidy. Their achievements in geology, palaeontology, cartography, and other fields put them among the most influential scientific institutions of the period.

Of all these scientific forays to the West, the 1871 expedition by geologist Ferdinand Hayden to the Yellowstone country has left perhaps the most visible legacy. Hayden's reports of this and later expeditions were mass-produced and widely read, and did much to bring Yellowstone scenery into middle-class drawing-rooms. Hayden was accompanied by a large retinue, which included William Henry Jackson, the photographer who first captured much of the Yellowstone country on plates, and Thomas Moran, the artist whose paintings of Yellowstone's wondrous nature transfixed the public. Together, the geologist, photographer, and artist did much to convince U.S. legislators that Yellowstone should be made a national park - the first in the United States - and, subsequently, to persuade Americans to visit it.

Yet, for all the importance of Hayden's first expedition, we know little about how it operated, or what the party actually did from day to day. Oddly, neither Hayden, Jackson nor Moran kept a diary that survived. It is as if the early nineteenth-century explorers Meriwether Lewis and William Clark had ventured on their mission along the Missouri River to the Pacific and then lost their notes. Marlene Deahl Merrill's edited version of the journals of two other members of the team, geologist George Allen and mineralogist Albert Peale, thus fills an important gap, and constitutes the first daily account of the historic 1871 Yellowstone Survey. These journals are, in fact, the only diaries of the expedition known to exist. Integrated here with selections from Allen's field notebook and letters that Peale wrote to newspapers during the expedition, they form a valuable addition to our knowledge of the survey.

This is a good thing, for previous accounts (most of them written by Hayden and Jackson years later) contain substantial errors. Jackson, for example, recalls in his autobiography that the Hayden party in 1871 was the first group of white men to visit Mammoth Hot Springs, one of the park's central features. How striking, then, to read here that when the party arrived they were met by two white settlers who had claimed the springs and were bent on turning them into a resort for health-seekers - such as the syphilitics who were also there to greet the expedition.

Hayden himself, for a host of reasons, discounted Indian claims to the Yellowstone region, and contributed to the myth of Yellowstone as an "uninhabited wilderness". In his journal, Peale reports sightings of Indians, and writes of the precautions the party took against Indian attack. (The worry about Indian attack was probably needless, but an idea of what the Indians in question might have looked like is given by a photograph of a family of Bannock Indians taken by Jackson shortly after he left Yellowstone.)

Here, too, are glimpses of the scientific expedition's little-known support staff, people who are invisible in the official reports, including guides, horse wranglers, a driver nicknamed "Dummy" and a Mexican-American hunter known only as "Jos".

This is more than a compilation of journals, however. Interspersed between Allen's sentimental maundering and Peal's scientific enthusiasm are a number of letters from Hayden to Spencer Baird, the assistant secretary of the Smithsonian Institution, reporting on the expedition's progress. Pen-and-ink panoramas of the Yellowstone country, executed by the highly skilled (and self-taught) expedition topographer Henry Elliott grace the headings of each of the 10 chapters, and the work throughout is illustrated with well-chosen photographs by Jackson.

Merrill's editing is superb. In 47 pages of endnotes, she integrates the journals with historical and scientific scholarship about Yellowstone and the American West. The achievements of the expedition become as salient as its curious errors, which include the mismeasuring of various peaks and geological features. The glossary of scientific terms is most helpful to the novice, and the four appendices (which include capsule biographies of expedition members) help flesh out the piece. Those wanting to know about Yellowstone at the time it became a national park have long relied on Hayden's official reports. Now that body of work has an important supplement. Nobody who seeks a deeper understanding of Yellowstone's natural systems as they were in 1871, or how nineteenth-century science was yoked to westward expansion, should miss this remarkable piece of editing and scholarly reconstruction.

C. STUART HOUSTON

863 University Drive, Saskatoon, Saskatchewan S7N 0J8, Canada

News and Comment

The 123rd Annual Business Meeting of The Ottawa Field-Naturalists' Club: 8 January 2002

The 123rd Annual Business Meeting of The Ottawa Field-Naturalists' Club will be held in the auditorium of Victoria Memorial Museum (Canadian Museum of Nature), McLeod and Metcalfe streets, Ottawa, on Tuesday 8 January 2002 at 7:30 p.m. (19:30 h). The Council for 2002 will be elected at this meeting and a brief review of the activities during 2001 will be given, as well as a statement of the Club's finances.

KEN ALLISON
Recording Secretary

Call for Nominations: The Ottawa Field-Naturalist's Club 2002 Council

Candidates for Council may be nominated by any member of The Ottawa Field-Naturalist's Club. Nominations require the signature of the nominator and a statement of willingness to serve in the position for which nominated by the nominee. Some relevant background information on the nominee should also be provided.

COLIN GASKELL
Chair, Nominating Committee

Call for Nominations: The Ottawa Field-Naturalists' Club 2001 Awards

Nominations are requested from members of The Ottawa Field-Naturalists' Club for the following: Honorary Membership, Member of the Year, George McGee Service Award, Conservation Award: Member, Conservation Award: Non-member, and the Anne Hanes Natural History Award. Descriptions of these awards have appeared in *The Canadian Field-Naturalist* 113(4): 689. With the exception of nominations for Honorary Member and Conservation Award: Non-member, all nominees must be members of The Ottawa Field-Naturalist Club in good standing.

IRVIN BRODO
Chair, Awards Committee

Point Pelee Natural History News 1(1) Spring 2001

The first issue of a natural history newsletter for Point Pelee, Ontario, edited by Alan Wormington (e-mail: wormington@juno.com) contains features by Wormington, Alfred H. Rider, Henrietta T. O'Neil and Sarah Rupert: In the Beginning — The Point Pelee Natural Heritage Research Committee — The 2000 Invasion of Zebra Swallowtails at Point Pelee — Pawpaw at Point Pelee — Noteworthy Bird Records: August 2000 to February 2001 — Early Migrants at Point Pelee: Spring 2001 — Point Pelee Butterflies: Annual Summary for 2000 — Eurasian Teal: A new species for Point Pelee? — Point Pelee Christmas Bird Count: December 18, 2000 — Recent Additions to Point Pelee's "Checklist of Birds", and sections: In the Field, News and Announcements, Upcoming events and outings [April-May-June].

Subscription rates are Canada: CAN $15 (one year) or $30 (two years); International: US $15 (one year) or $30 (two years). Send payment (and e-mail address, optional) to The Friends of Point Pelee, 1118 Point Pelee Drive, Leamington, Ontario N8H 3V4. Issues will be mailed in March, June, September, and December, and back issues will be available for $15 per Volume/ $5 per issue (postage paid).

Alberta Wildlife Status Reports: (26 to 31)

The Fisheries and Wildlife Management Division of the Alberta Natural Resource Status and Assessment Branch, Alberta Environmental Protection, has released new Wildlife Status Reports. The Series Editor is Isabelle M. G. Michaud, the Senior Editor is David R. C. Prescott, and the illustrations are by Brian Huffman. For a listing earlier numbers in the series, see *The Canadian Field-Naturalist* 112(1): 169 for 1-11; 113(2): 311 for 12-17; 113(4): 686 for 18-21; and 114(1): 151 for 22-25. Recent reports issued in 2000 and 2001 are:

26. Status of the Trumpeter Swan (*Cygnus buccinator*) in Alberta, by Richard D. Lauzon. 17 pages.
27. Status of the Pygmy Whitefish (*Prosopium coulteri*) in Alberta, by William C. Mackay. 16 pages.
28. Status of the Short-eared Owl (*Asio flammeus*) in Alberta, by Kort M. Clayton. 15 pages.
29. Status of the Willow Flycatcher (*Empidonax traillii*) in Alberta, by Bryan Kulba and W. Bruce McGillivray. 15 pages.
30. Status of the Woodland Caribou (*Rangifer tarandus caribou*) in Alberta, by Elston Dzus. 47 pages.
31. Status of the Western Spiderwort (*Tradescantia occidentalis*) in Alberta, by Bonnie Smith. 12 pages.

For copies contact the Information Centre - Publications, Alberta Environmental Protection, Natural Resources Service, Main Floor, Great West Life Building, 9920 - 108 Street, Edmonton, Alberta T5K 2M4, Canada (telephone: (780) 422-2079), or Information Service, Alberta Environmental Protection, #100, 3115 - 12 Street NE, Calgary, Alberta T2E 7J2, Canada (telephone: (403) 297-3362); or Sherry Feser, 7th Floor, O. S. Longman Building, 6909 - 116 Street, Edmonton, Alberta T6H 4P2: telephone (780) 427-1248; fax (780) 422-9685; e-mail sherry.feser@gov.ab.ca

The Boreal Dip Net 5(2)

The March 2001 issue of the Newsletter of the Canadian Amphibian and Conservation Network/ Reseau Canadien de Conservation des Amphibiens and Reptiles (http://eqb-dqe.cciw.ca/partners/carcnet/intro.html). Contents: Notes from the editor — Ontario Herp Summary: an update — Depositing your data — New Books to get — Some other meeting announcements — Terrestrial salamanders need woody debris — P.E.I. Annual Meeting: an announcement — An ambystomatid coping at northern extremes — Sharp-tailed Snake study — Excerpts from Herp News — Membership/Donation forms.

For membership and other information on the CARCN/RCCAR contact Bruce Pauli, Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Boulevard, Hull, Quebec, Canada K1A OH3.

Froglog: Newsletter of the Declining Amphibian Populations Task Force (43, 44)

Number 43, February 2001, contains: Surveillance of Amphibian Populations for Infectious Diseases (Rick Speare, Diana Mendez, Lee Berger, and Alex Hyatt) — Poorly Known Endemic Amphibians of Northeast India (Md. Firoz Ahmed) — Induction of Cell Death by Synthetic Pyrethroid Insecticide Cypermethrin in the Developing Brain of *Physalaemus biligonigerus* tadpoles from Argentina (M. F. Izaguirre, R. C. Lajmanovich, P. M. Peltzer, A. Peralta Soler and V. H. Casco — CARCNET/ RRCR Update (Christine Bishop) — Froglog Shorts — Publications of Interest.

Number 44, April 2001, contains: Ultraviolet (UV) radiation and the decline of amphibian populations in Central Spain (Miguel Lizana and Adolfo Marco — The Crested Newt (*Triturus cristatus*): Distribution, Biology, Ecology and Protection: 11-12 November 2000, Rostock, Germany (Richard A. Griffiths) — Monitoring Protocols Working Group Report (Richard A. Griffiths) — Amphibian harvesting in Romonia (Nemes Szilard and Kovasznay Csengele — Froglog Shorts — Publications of Interest.

Froglog is the bi-monthly newsletter of the Declining Amphibian Populations Task Force of the World Conservation Union (IUCN)/Species Survival Commission (SSC) and is supported by the Open University, The World Congress of Herpetology, the Smithsonian Institution, and Harvard University. The newsletter is edited by John W. Wilkinson, Department of Biological Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail: daptf@open-ac.uk. Funding for *Froglog* is underwritten by the Detroit Zoological Institute, P.O. Box 39, Michigan 48068-0039, USA. Froglog can be accessed at http:/www2.open.ac.uk/biology/froglog/

Frog Log 1(1): A newsletter for Canadian "Frogwatch"

The inaugral (Spring 2001) issue of the Canadian newsletter *Frog Log* (not to be confused with the long-standing international newletter *Froglog*, see above) is a new project of the Canadian Nature Federation designed to keep participants in the (Canadian) "Frogwatch" inititive informed and up-to-date on program developments. Frogwatch is a joint program of Environment Canada's Ecological Monitoring and Assessment Network (EMAN) and the Canadian Nature Federation. This issue of the newsletter features: How to get involved, Frog-watching tips, Frog-Faqs, What's in a Name?, Frog Facts & Folklore. Coming this fall will be another Nature Watch program: "Wormwatch" (see fall, *Nature Canada* for details. For more information on Frogwatch, check EMAN site at http://www.cnf.ca/frog/. To obtain printed copies of the national Frogwatch identifiacation poster (in English or French) and the Frogwatch newsletter contact: Canadian Nature Federation, 1 Nicholas Street, Suite 606, Ottawa, Ontario K1N 7B7 Canada; e-mail: frogwatch@cnf.ca

Marine Turtle Newsletter (92)

The April 2001 issue, 36 pages, contains: EDITORIAL: Making the books balance and a look at the future — ARTICLES: Update the Kemp's Ridley Turtle Nesting in Mexico — Evaluation of the Black Turtle Project in Michoacan Mexico — Nest morphology in the Leatherback Turtle — Using GIS for Sea Turtle research at the Fog Bay rookery in northern Australia — Eastern Mediterranean 'holiday hotspots' versus sea turtle 'nesting hotspots' — NOTES: From hook to hook: The odyssey of a Logerhead Sea Turtle in the Mediterranean — MEETING REPORTS — ANNOUNCEMENTS — NEWS & LEGAL BRIEFS — RECENT PUBLICATIONS.

The Marine Turtle Newsletter is edited by Brendan J. Godley and Annette C. Broderick, Marine Turtle Research Group, School of Biological Sciences, University of Wales, Swansea, Singleton Park, Swansea SA2 8PP Wales, United Kingdom; e-mail MTN@swan.ac.uk; Fax +44 1792 295447. Subscriptions to the MTN and donations towards the production of MTN and its Spanish edition NTM [Noticiero de Tortugas Marinas] should be sent to Marine Turtle Newsletter c/o Chelonian Research Foundation, 168 Goodrich Street, Lunenburg, Massachusetts 01462 USA; e-mail RhodinCRF@aol.com; fax + 1 978 582 6279. MTN website is: <http://www.seaturtle.org/mtn/>.

Editor's Report for Volume 114 (2000)

Mailing dates for issues in volume 114 were: (1) 7 March 2000, (2) 7 September 2000, (3) 27 December 2000, (4) 4 May 2001. Totals for circulation to members of the Ottawa Field-Naturalists' Club and individual and institutional subscribers to *The Canadian Field-Naturalist* in 2000 together with those of 1999 are given in Table 1. The number of articles and notes in volume 114 is summarized in Table 2 by topic; totals for Book Reviews and New Titles are given in Table 3, and the distribution of content by page totals per issue in Table 4. An important aid to publication was created by Council decision to make 80% of the annual interest from the capital of the Thomas Manning bequest available to *The Canadian Filed-Naturalist* to offset the publication cost of northern papers where other funds (authors and institutional contributions) are insufficient to cover the page charges. This was made retractive to 1999, and in 2000 Council approved fund expenditures of totalling $1430: in 113(3): 375-385, $835 of the cost for the paper "Important bird and mammal records in the Thelon River Valley, Northwest Territiories: Range expansion and possible caunses"; in 113(4): 641-645 all of the $475 cost of publication for "Maritime Quillwort, *Isoetes maritima* (Isoetaceae) in the Yukon Territory"; and 663-664 all of the $120 cost of "Frogs consumed by Whimbrels, *Numenius phaeopus*, on breeding grounds at Churchill, Manitoba"

St. Joseph M.O.M. Printers, 300 Parkdale Avenue, Ottawa, set and printed the journal and special thanks are due Emile Holst, and to the Pre-press section particularly Yolande and Cecilia, and all the the MOM staff whose efforts make each issue possible. Wanda J. Cook proof-read the galleys and Bill Cody as Business Manager handled all reprint requests and bills and oversaw and proofed the compilation of the Index prepared by Leslie Durocher. Wilson Eedy continued as Book-Review Editor.

Manuscripts (excluding book reviews, notices, club or journal reports) submitted to *The Canadian Field-Naturalist* totalled 154 in 2000, a substantial increase from recent years, 30 more than the previous year and 41 more than the year before, and not topped since 1975 (when 167 manuscripts were submitted). Unfortunatly this influx contributed to a slowing in the processing of papers, and substantial delays in their return. We expect to be caught up before the end of 2001. It has also meant an internal reconsideration by the editor of existing acceptance criteria for papers, both by content, region, and ability to share costs of publication, but no change in our long-standing policies and broad focus are contemplated at the present time. I am most grateful for the consideration, general good-will and patience extended by the many supportive authors for whom publication in *The Canadian Field-Naturalist* is important.

The following returned reviews in 2000: *Associate Editors*: Birds: A. J. Erskine, Canadian Wildlife Service, Sackville, New Brunswick (40); Earl Godfrey, Nepean, Ontario; Botany: Charles D. Bird, Erskine, Alberta (18); Paul M. Catling, Agriculture and Agri-food Canada, Ottawa (14); Entomology: R. Anderson Canadian Museum of Nature (2); Fish and Marine Mammals: Robert R. Campbell, Ottawa, Ontario (7); Fish: Brian W. Coad, Canadian Museum of Nature, Ottawa, Ontario (3); Mammalogy: W. O. Pruitt, Jr., University of Manitoba, Winnipeg (40); Warren B. Ballard, Texas Tech University, Lubbock (37). *Additional reviewers*: L. Adams, U.S. Geological Survey, Ancorage, Alaska; S. Aiken, Canadian Museum of Nature, Ottawa; R. Anderson, Seattle Aquarium, Washington; C. D. Ankney, University of Western Ontario; C. Braun, Colorado State University, Fort Collins; J. Barr, University of Guelph, Ontario; E. Bayne, Canadian Wildlife Service, Saskatoon; G. V. Byrd, U. S. Fish and Wildlife Service, Adak, Alaska; J. R. Bider, MacDonald College of McGill University and Ecomuseum, Montreal (2); R. Bird, British Antarctic Survey, Cambridge, England;

TABLE 1. The 2000 circulation of The Canadian Field-Naturalist (1999 in parenthesis). Membership totals from Annual Report of the Ottawa Field-Naturalists' Club, January 2001; subscription totals compiled by W. J. Cody. Forty percent of membership dues and 100% of subscriptions go to publication of *The Canadian Field-Naturalist*. Members vote on Club affairs, subscribers and institutions do not.

	Canada		USA		Other		Totals	
Memberships								
Family & individual	910	(921)	32	(30)	6	(6)	948	(957)
Subscriptions								
Individuals	184	(184)	61	(62)	6	(7)	251	(253)
Institutions	178	(181)	255	(277)	38	(39)	491	(497)
Totals	362	(365)	316	(339)	44	(46)	742	(750)
TOTALS	1272	(1286)	348	(369)	50	(52)	1690	(1707)

Note: 22 countries are included under "Other" (outside Canada and United States): Austria, Belgium, Brazil, Denmark (2), United Kingdom (9: including 1 to Scotland), Finland (2), France (3: including 1 to St. Pierre & Miquelon), Germany (2), Iceland, Ireland, Japan, Mexico, Netherlands (3), New Zealand, Norway (4), Poland, Russia, South Africa, Spain (3), Sweden (2), Switzerland (2), Trinidad and Tobago.

TABLE 2. Number of articles and notes published in *The Canadian Field-Naturalist* Volume 114 (2000) by major field of study.

Subject	Articles	Notes	Total
Mammals	21	19	40
Birds	16	7	23
Amphibians + reptiles	4	1	5
Fish	5	1	6
Invertebrates	7	1	8
Plants	11	2	13
Tributes	3	0	3
Totals	67	31	98

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist* Volume 114 (2000) by issue.

	(1)	(2)	(3)	(4)	Total
Articles	141	124	161†	134	560
Notes	8	26	18	16	68
News and Comment	4	6	4	5	19
Tributes	11	0	0	6	17
Annual Meeting	0	0	7	0	7
Book Reviews*	21	7	13	9	50
Index	0	0	0	34	34
Advice to Contributors	1	1	1	0	3
Totals	186	164	204	204	758

†Includes a 21 page review article on status of amphibians and reptiles in Canda which appears after News and Comment.

*Total pages for book review section include both reviews and new titles listings.

D. A. Boag, Brendwood Bay, British Columbia; J. Bogart, University of Guelph, Ontario; S. Bondrup-Neilson, Acadia University, Wolfville, Nova Scotia; W. S. Boyd, Canadian Wildlife Service, Delta, British Columbia; M. Boulet, MacMaster University, Hamilton, Ontario; I. Brodo, Canadian Museum of Nature, Ottawa; R. J. Brooks, Unviversity of Guelph, Ontario (2); R. T. Brooks, U.S. Department of Agriculture, Amherst, Massachusetts; M. Cadman, Canadian Wildlife Service, Guelph; L. Carbyn, Canadian Wildlife Service, Edmonton; M. Crete, Ministre de l'Environment et de la Faune, Quebec; W. J. Cody, Agriculture and Agi-food Canada, Ottawa; J. Connelly, Idaho Department of Fish and Game, Pocatello; D. Christie, Albert, New Brunswick; A. Crowder, Queen's University, Kingston; A. W. Diamond, University of New Brunswick, Fredericton (2); D. Dunbar, British Columbian Ministry of Environment, Surrey; J. Duncan, Ministry of Natural Resources, Winnipeg, Manitoba; E. H. Dunn, Canadian Wildlife Service, Hull; D. S. Erskine, Willowdale, Ontario; A. O. Fortin, Montreal, Quebec; B. Theresa Fowler, Canadian Wildlife Service, Hull, Quebec; B. Freedman, Dalhousie Universitey, Halifax, Nova Scotia (2); T. D. Galloway, Department of Entomology, University of Manitoba, Winnipeg; A. J. Gaston, Canadian Wildlife Service, Hull, Quebec; J. Gillen, Nova Scotia Museum, Halifax (2); P. Goosen, Canadian Wildlife Service, Edmonton (2); S. A. Graham, Kent State University, Ohio; P. J. Gregory, University of Victoria, British Columbia (2); W. Grimm, Eastern Ontario Biodiversity Museum, Kemptville, Ontario; Eric Haber, National Botanical Services, Ottawa (2); R. L. Haedrich, Memorial University of Newfoundland, St. Johns; P. Hamilton, Canadian Museum of Nature, Ottawa; F. Harrington, Mount St. Vincent University, Halifax, Nova Scotia (2); J.

TABLE 3. Number of reviews and new titles published in Book Review section of *The Canadian Field-Naturalist* Volume 114 by topic.

	Reviews	New Titles
Zoology	24	84
Botany	4	22
Environment	16	58
Miscellaneous	4	24
Young Naturalists	1	66
Totals	49	254

D. Henry, National Parks Service, Haines Junction, Yukon; D. Hik, University of Alberta, Edmonton; G. Holord, Canadian Wildife Service, Edmonton; C. S. Houston, Saskatoon, Saskatchewan; R. James, Sutherland, Ontario (4); H. M. Jahns, Heirich Heine Universital, Dusseldorf, Germany; M. Jean, Centre St. Laurent, Montreal; W. Klenner, Kamloops, British Columbia; B. Kessell, University of Alaska Museum, Fairbanks; R. Lein, University of Calgary, Alberta; L. Licht, York University, Toronto, Ontario (2); J. Lien, Memorial University, Newfoundland; J. Mather, University of Lethbridge, Alberta; D. E. McAllister, Canadian Museum of Nature, Ottawa; R. McCulloch, Royal Ontario Musuem, Toronto (2); B. McCune, Oregon State Museum, Corvallis; B. McGillivray, Alberta Provincial Museum, Edmonton (2); D. McNicol, Candian Wildlife Service, Ottawa; D. J. Mech, North Central Forest Research Station, U. S. Geological Survey, St. Paul, Minnesota (3); R. W. Nero, Manitoba Natrual Resources, Winnipeg (2); J. D. McPhail, University of British Columbia, Vancouver; P. H. Martin, Canadian Wildife Service, Burnaby, British Columbia; J. Nelson, Unviersity of Alberta, Edmonton; D. J. Nettleship, Tantullon, Nova Scotia; M. J. Oldham, Ontario Natural Resources, Perterbough; M. Petrie, Ducks Unlimited, Memphis, Tennessee; S. Petrie, Long Point Waterfowl and Wetlands Research Fund, Port Rowan, Ontario; P. J. Pietz, Northern Prairie Wildlife Research Centre, Jamestown, North Dakota; C. Renaud, Canadian Museum of Nature, Ottawa; A. A. Reznicek, University of Michigan, Ann Arbor; J. D. Rising, University of Toronto, Ontario; G. R. Robertson, Canadian Wildlife Service, Delta, British Columbia (2); L. Rogers, Northwoods Research Centre, Ely, Minnessota; J. Romo, University of Saskatchewan, Saskatoon; D. Schecl, Alaska Pacific University, Anchorage; M. Schroeder, Washington Department of Fish and Game, Bridgeport; F. W. Schueler, Eastern Ontario Biodiversity Museum, Kemptville, Ontario (2); B. Scott, Kingston, Ontario (2); G. Scudder, University of British Columbia, Vancouver; S. C. Sealey, University of Manitoba, Winnipeg; K. W. Stewart, University of Manitoba, Winnipeg (2); I. Thompson, Canadian Forest Service, Saulte Ste. Marie, Ontario (8); R. Titman, MacDonald College of McGill University, Montreal; D. H. Vitt, University of Alberta, Edmonton; R. Weeber, Bird

Studies Canada, Port Rowan, Ontario; T. I. Wellicome, Canadian Wildlife Service, Edmonton.

Once again, I am also indebted to Eleanor Zurbrigg, President of the Ottawa Field-Naturalists' Club and the Club Council for continuing support of the journal; Chairman Ron Bedford and the Publications Committee of the OFNC for editorial encouragement and support, to the Canadian Museum of Nature for access to its library and the facilities at the Natural Heritage Building, 1740 Pink Road, Aylmer, Quebec, and to Joyce for everything else. Special acknowledgment and best wishes are due to Dr. Warren B. Ballard, who steped down at end of the year 2000 as an associate editor for mammalogy to assume editorial duties with another journal. His advice and encouragement, like that of all the associate editors, has meant a great deal to me.

FRANCIS R. COOK
Editor

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